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Mammals of the Graham (Pinaleno) Mountains, Arizona

Donald F. Hoffmeister

Museum of Natural History, University of Illinois, Urbana

Much of Arizona is a desert, broken intermittently by mountain ranges, more or less isolated, one from the other. Many of these ranges do not rise high enough above the desert floor to have a flora or fauna appreciably different than that of the surrounding desert. In southeastern Arizona, however, there are several isolated ranges that rise abruptly several thousand feet above the desert and have a vegetative cover of a boreal type, which is markedly different from that of the adjacent desert. These are veritable islands, with a distinctive flora and fauna, within a sea-like desert. Within these "islands" there is a diversity of ecological niches, extreme variation altitudinally in a short distance. and complete or nearly complete isolation.

Most notable of these island-like mountain ranges in southeastern Arizona are the Chiricahuas, Huachucas, Santa Catalinas, and Grahams or Pinalenos. Only one of these ranges—the Grahams—has not had its mammalian fauna intensively studied. Therefore, during two summers (1951-2) 164 man days were spent by our field parties studying and collecting mammals in the Grahams. In all 1,081 specimens were preserved as study skins.

The Grahams or Pinalenos are situated in southeastern Arizona, within fifty miles of New Mexico and within 100 miles of old Mexico, and entirely within Graham County. They are bounded by the Sulphur Springs-Arivaipa Valley to the south and west, Gila Valley to the north, and San Simon Valley to the east. These valleys have an average elevation of about 3,200 feet. From the valley floors, the Grahams rise rather abruptly to a crest of between 8,500 and 10,000 feet. Three peaks rise above this crest—Mt. Graham, 10,713 feet; Heliograph, 10,028 feet; Webb, 10,029 feet.

The base of the Mountains and the alluvial fans are covered with mesquite, prickly pear, cholla, yucca, grama, and certain other Lower Sonoran-zone plants. Near the eastern base of the Mountains along the Swift Trail, at 3,975 feet elevation, the annual precipitation is 13.04 inches, according to Martin and Fletcher (1943). In this same zone, but at the western base of the Mountains, at Fort Grant, 4,950 feet, the annual precipitation was 14.35 inches over a 62-year period, with an annual total snowfall of 4.6 inches, and a mean, minimum, and maximum temperature of 61.6°F, 7°F, and 111°F, respectively.

Above the mesquite-grama belt, there appear Emory and Arizona oaks, junipers, manzanita, agave, grama, and side oats. Still higher, the woodland becomes more dense, with many silverleaf oaks, Chihuahua and ponderosa pines, Arizona oaks and manzanitas. In general, this is the oak-woodland zone. Within the conifer belt, but at its lower edge, ponderosa pine predominates,

together with Douglas fir, some white fir, and oaks. Here, as at Turkey Flat, 7,500 feet, the annual precipitation exceeds twenty inches (23.73, according to Martin and Fletcher, 1943), and there are several feet of snow annually. The higher parts of the coniferous belt have white and alpine firs, Douglas fir, white and limber pines, ponderosa pine, and some aspen. On the highest peaks, Engelmann's spruce is present together with aspen, fir, limber pine, and Douglas fir. Here, total annual precipitation is considerable, for snowfall amounts to several feet, with snow remaining on some sides of Mt. Graham well into the summer. Heald (1951) has well emphasized the variation in temperatures from the base of the Grahams to the summit—a variation of 56°F, with a temperature in late June of 108°F at the base, 52°F on the top of Mt. Graham, and all within an airline distance of less than ten miles.

Within the coniferous forest, numerous mountain meadows, each consisting of a few acres, are present. These almost invariably have a small stream running through them and have a grassy cover. Encroachment of shrubs and trees appears to be slow. These meadows are the principle habitat of *Sorex vagrans, Reithrodontomys megalotis, Microtus longicaudus,* and *Thomomys bottae,* the hunting grounds for numerous kinds of bats, and the feeding and resting sites for *Odocoileus virginianus couesi.*

Many persons have aided in the field work. Foremost in this regard is Woodrow Goodpaster, whose industry, enthusiasm, keen field observations, and bountiful collecting have added so much to this report. Lois Goodpaster forms the other member of this successful team. Steve Gallizioli, game biologist of the Arizona Game and Fish Commission, has provided detailed information on the plants in the Grahams, much data on mammals, and given much other help. Others who have aided greatly in the field work are: Robert T. Calef, David E. Comings, Charles A. McLaughlin, and Richard G. Van Gelder. The cordial hospitality and facilities placed at our disposal by the Dee Jernigans and the Galliziolis made our work more pleasant and successful. The Arizona Game and Fish Commission, through John Hall, A. W. Yoder, O. N. Arrington, and W. G. Swank has aided us, as has Earl Long of the U. S. Fish and Wildlife Service. Mr. Allen G. Watkins, forest supervisor, Crook National Forest, kindly provided us with information about the Graham Mountains and extended us the hospitality of the Forest Service. To these, and the many others in the Mountains, who have provided us with information about the mammals, we are most grateful.

All measurements used in the text are in millimeters unless otherwise indicated. Capitalized color terms are taken from Ridgway (1912). All specimens, unless otherwise indicated, are in the Museum of Natural History, University of Illinois.

GAZETTEER OF COLLECTING LOCALITIES IN THE GRAHAM MOUNTAINS

All localities in Graham County (fig. 1)

1. South Taylor Canyon, approximately 2 mi. N 76 Ranch: oak woodland habitat, with Emory and Arizona oaks, juniper, mountain mahogany, some Chihuahua pine, manzanita, squaw-bush (*Rhus trilobata*), and silk- tassel (*Garrya wrightii*).
2. 76 Ranch, 5300 feet: desert shrub type, just below the tree belt; mesquite with burro-weed (*Applopappus*)—snake-weed (*Gutierrezia*) understory, catclaw (*Acacia greggii*), and *Lycium*.
3. Haunted Ranch, 3½ mi. NW Ft. Grant, 4900 feet: mesquite, sparse grass, rocky soil.

Fig. 1.—The Graham Mountains and surrounding deserts. Collecting localities are numbered (see Gazetteer) and the peaks, passes, and roads are indicated.

4. One mile NE Ft. Grant, 5100 feet (in Grant Creek Canyon): desert shrub habitat, with Emory, Arizona, and scrub oaks, sycamore, ash, some mesquite, and catclaw; snake-weed and burro-weed ground cover.

5. One-third mile SE Ft. Grant, 4750 feet: desert shrub type; tall, thick mesquite, with understory of burro-weed and snake-weed; scattered *Lycium* and catclaw.

Fig. 2.—Desert grassland between Bonita and Ft. Grant, with grasses and sacaton in foreground; beargrass, yucca, and mesquite in background. This grassy area is the preferred habitat of desert cottontails, cotton rats, white-throated wood rats, spotted ground squirrels, and western harvest mice. Photograph by Woodrow Goodpaster.

Fig. 3.—Desert-shrub habitat near Bonita, with an understory of burro-weed and

6. Three-fourths mile SE Ft. Grant, 4750 feet: desert shrub type; collecting done in patch of high, green weeds resembling lambs-quarters.

7. One and one-half miles SW Ft. Grant, 4600 feet: desert shrub-grassland habitat (fig. 2), with yucca, mesquite, some sacaton (*Sporobolus wrightii*), sparse grass, cholla cactus, scattered ash, *Lycium*, burro-weed, and snake-weed.

8A. Two miles NW Bonita, 4600 feet (along Bonita-Aravaipa road): grassland type, with a few widely scattered mesquites, yuccas, *Lycium*, and prickly pear.

8B. One-half mile NW Bonita: grassland type, with tumbleweeds along fence, yucca, some mesquite, sacaton, and burro-weed.

9. Bonita, 4540 feet: trapping done northeast of store, along road toward Ft. Grant, among sacaton, bordered by mesquite and grazed field, with scattered yuccas and salt-bush (*Atriplex canescens*).

10. Three-fourths mile SE Bonita, 4576 feet, near road where it crosses Pitchfork Creek: desert shrub type (fig. 3) with mesquite, sunflower, burro-weed, and snake-weed.

11. Three miles S Ft. Grant, 4600 feet (fig. 4): yucca, mesquite, burro-weed, and snake-weed.

12. Three miles E Bonita, 4700 feet: shrubby mesquite, burro-weed, snake-weed, scattered plants of buckwheat (*Eriogonum wrightii*), and yucca.

13. Three and one-half miles E Bonita, 4800 feet: same as 12, but no yucca.

14. Pitchfork Ranch, 5350 feet [5 mi. E, 1 mi. N Bonita]: oak woodland type, with Emory oaks, juniper, mountain mahogany, manzanita, and squaw-bush.

15. Stockton Pass Campground, 5725 feet: large grassy areas with Emory oaks, junipers, manzanita, and squaw-bush.

16. One-half mile W CN Ranch, 5000 feet: Emory oaks, juniper, bear grass (*Nolina*), buckwheat, and some perennial grasses.

17. CN Ranch, 4900 feet: clearing in oak woodland belt, with burro-weed, Emory oaks, some junipers, sycamores, ash, black walnut, rabbit-brush (*Chrysothamnus nauseosus*), bear-grass, manzanita, and *Lycium*.

18. Two and one-half miles S, 1 mi. E Maverick Mtn., 4500 feet: mesquite, prickly pear cactus, yucca, some agave, burro-weed, squaw-bush, and catclaw.

19. Gillespie Wash, 4300 feet [="Gillespie" of Crook National Forest map; along Gillespie Wash, 2/3 mi. north of Stockton Pass road crossing mountains to Bonita]: mixture of sycamore, ash, seep-willow (*Baccharis glutinosa*), cottonwoods, buck-brush (*Ceanothus greggii*), snake-weed, and burro-weed along Wash; prickly pear, agave, sotol (*Dasylerion wheeleri*), ocotillo, and shrubby mesquite on side hills.

20. Jernigan Ranch, 4500 feet (along Gillespie Wash, 1 mi. S road to Bonita; labelled Boscoe on Crook Ntl. Forest map): desert shrub type (fig. 5), with mesquite, cacti, and perennial grasses.

21. Eight miles S, ½ mi. W Artesia, 4200 feet (1/5 mi. inside Crook Ntl. Forest, along Stockton Pass Road): desert shrub type, with shrubby mesquite, prickly pear, yucca, cholla, sparse grass, burro-weed, snake-weed, catclaw, and some juniper.

22. Six miles SSW Pima, 2900 feet (sometimes called "Bird Farm"): desert shrub type, with mesquite, yucca, cholla, tumbleweed, snake-weed, burro-weed, catclaw, and some cottonwoods; along a creek, usually dry, some ash, willow, and seep-willow.

23. Eight miles SSW Pima, approximately 3000 feet (Upper reservoir): desert shrub type, with mixture of snake-weed, burro-weed, creosote bush, and scattered shrubby mesquite.

24. Lebanon Reservoir no. 2: 6 mi, S, 2 mi. W Safford, approximately 3500 feet.

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snake-weed intermixed with catclaw, yucca, *Lycium*, and mesquite. Mammals found in such a habitat include the desert pocket mouse, northern grasshopper mouse, white-footed mouse, and cactus mouse. Photograph by Woodrow Goodpaster.

Fig. 4.—Yuccas intermixed with burro-weed, snake-weed, and white horse-nettle, along Stockton Pass road, 3 mi. S Ft. Grant. Photograph by Woodrow Goodpaster.

25. Marijilda Canyon campground, 4400 feet: desert shrub type, with oak woodland extending along stream (dry 6-8 months of year); mixture of mesquite, sycamore, ash, Emory oak, grape, hackberry, and buck-thorn (*Rhamnus crocea*) along stream; prickly pear, cholla, scrub oak, ocotillo, barrel cactus, agave, *Lycium*, and ratany (*Krameria*) on side hills.

LOCALITIES ALONG OR NEAR SWIFT TRAIL

26. One-fourth mile S Cyclone Hill, 3900 feet: desert shrub type, primarily mesquite, with burro-weed and snake-weed ground cover, scattered catclaw, ocotillo, *Lycium*, and perennial bunch grasses.

27. Angle Orchard Ranch, 5120 feet: oak woodland habitat, with trapping done in tall grass of fruit orchard which is surrounded by Arizona and Emory oak, juniper, mahogany, and silk-tassel.

28. Noon Creek campground, 5450 feet: oak woodland habitat with Arizona and Emory oak, seep-willow, ash, squaw-bush, willow along stream (dry most of the year); manzanita, juniper, on side hills.

29. Wet Canyon, 6050 feet (collecting done just above picnic grounds): a cool canyon with a continuous flow of water in the creek, silverleaf oak, sycamore, Chihuahua pines, Arizona alders, black walnuts, big tooth maples, and box elders associated with snowberry and ninebark (*Physocarpus monogynus*).

30. Cluff Farm, 6950 feet: lower edge of pine belt, with silverleaf oak, Chihuahua pine, juniper, box elder, snowberry, ninebark, and rock-spiraea (*Holodiscus dumosus*); collecting done around area cleared on rocky mountainside for gardening.

31. Turkey Flat, 7400 feet [=Pinecrest of some maps]: mixture of yellow pine, Douglas fir, white fir, aspen, Gambel oak, hoptree (*Ptelea angustifolia*), snowberry, bracken, and some grasses.

Fig. 5.—Desert shrub habitat near base of Mountains, with beargrass, catclaw, rabbitbrush, mesquite, *Lycium*, and agave; photographed near Jernigan Ranch. Mammals found in such a habitat include Western pocket gophers, Bailey pocket mice, Merriam kangaroo rats, antelope ground squirrels, cactus mice, and desert cottontails. Photograph by Woodrow Goodpaster.

32A. Heliograph Peak, 2/5 mi. S, 8900 feet: sparse, open forest of limber pine, alpine fir, aspen, thimbleberry, snowberry, some bracken, and some grasses.

32B. Heliograph Peak, 1 mi. S, 8900 feet: open forest of small limber pine, brush, including thimbleberry (*Rubus neomexicanus*), some bracken, some grasses.

33. Snow Flat, 8750 feet (1 mi. W, 1/4 mi. N Heliograph Pk.): large, grassy meadow surrounded by yellow and limber pine, white fir, Douglas fir, snowberry, with a small stream entering pond at lower end of meadow.

34. Treasure Park, 8950 feet (1/8 mi. S Swift Trail; 3 mi. S Mt. Graham): a large, grassy meadow, surrounded by yellow and limber pine, Douglas fir, white fir, aspen, and thin-leaf alder along stream; small trickle of water runs through the meadow.

35. Hospital Flat, 9000 feet: a large, grassy meadow, with good stand of perennial grasses, numerous mature yellow and limber pines, Douglas fir, white fir, scattered aspen, and thin-leaf alder along stream, all encroaching on meadow.

36. Hospital Flat Forest Camp, 9100 feet (picnic area and campground, 1/4 mi. N Swift Trail and approximately 1/4 mi. E Hospital Flat): along Big Creek, with a small amount of grass, numerous mature yellow and limber pines, Douglas fir, and white fir.

37. Columbine Ranger Station, 9500 feet: trapping done in heavy stands of yellow and limber pines, Douglas fir, white and alpine firs, aspen, thin-leaf alder, snowberry, Gambel oak; trapping done also in grassy meadow.

38. One-third mile W Columbine Ranger Station, 9400 feet: a grassy meadow at junction of roads to Webb Peak and Clark Peak; a creek, tributary to Soldier Creek, runs through this meadow; vegetation as in No. 37.

39. Soldier Creek, 9400 feet: near campground along Creek; a lush, grassy meadow (fig. 7), with small stream of water through it; meadow surrounded by heavy stand of conifers.

40. Head Soldier Creek, 9500 feet (to north of Swift Trail, near junction of Webb Peak and Clark Peak roads): trapping done along grassy slopes grown up with sneeze-weed (*Helenium hoopesii*) and perennial grasses; surrounding trees same as in No. 37.

41. Webb Peak, 10,000 feet (at top of Peak): among Douglas fir, pines, aspens, a few spruce, and numerous rocky outcroppings.

42. Goudy Creek Canyon: grassy, dry meadow, without water; trees as at Columbine.

43. Chesley Flat, 9300 feet: fairly dry meadow with water near the lower end on south side of road only; trees and shrubs as at Columbine.

44. Clark Peak, 1 mi. E, 8800 feet (fig. 6): along road, among Douglas fir, yellow pines, and aspen, with numerous large, rocky outcroppings.

Sorex vagrans monticola Merriam. Vagrant shrew.—Shrews, all of this species, were taken in the meadows and flats near the crest of the Mountains. They occurred among the tall grass where it grew along small streams coursing through the meadows. In these places, vagrant shrews were closely associated with long-tailed voles, *Microtus longicaudus leucophaeus,* and western harvest mice, *Reithrodontomys megalotis*. Shrews were much less abundant than the voles but as common as, or even more common than, the harvest mice. Much lower down the Mountains, at 6000 feet along Wet Canyon, specimens were taken near a stream and among boulders, leaf mold, and trees. No grass was present here. Five specimens have been taken near the head of Marijilda Canyon, among skunk cabbage, sedge, grasses, and brush (see Hall, 1932). Two specimens from near the head of Ash Creek, 9200 feet elevation, are in the U.S. Fish and Wildlife Service collection.

Sorex melanogenys was described (Hall, 1932) from Marijilda Canyon, 8600 feet, Graham Mountains. In 1934, Hall pointed out that this species was a member of the *Sorex vagrans* group and placed *S. melanogenys* as a synonym of *vagrans monticola*. He mentioned that in "*melanogenys*" the

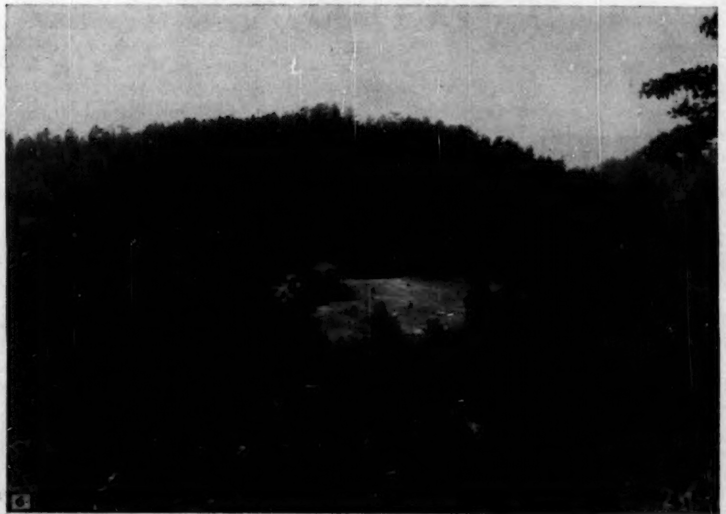

Fig. 6.—Alpine meadow surrounded by coniferous forest on Clark Peak. Trees include yellow and limber pines, white and alpine firs, and Douglas fir. In the meadow are found western pocket gophers, long-tailed voles, vagrant shrews, western harvest mice; in the forest, brush mice, deer mice, spruce squirrels, Abert squirrels, and eastern cottontails. Photograph by Woodrow Goodpaster.

Fig. 7.—Meadow edge, along Soldier Creek, with perennial grasses in foreground, including brome, fescue, bluegrass, and thistle; trees in background include white fir, Douglas fir, and yellow (ponderosa) pine. Photographed 1/3 mi. W Columbine Ranger Station by Woodrow Goodpaster.

third unicuspid was large in comparison with the fourth unicuspid ("has a greater anteroposterior length than in any other specimen of *Sorex vagrans monticola* I have examined"). In five specimens from the Huachuca Mountains, the third unicuspid is as large or larger than the fourth (Hoffmeister and Goodpaster, 1954). In skulls of the seven specimens collected by us in the Grahams, four have the third and fourth unicuspids of about the same size; in three, the third unicuspid was only slightly smaller than the fourth. In the Santa Rita (one specimen) and Chiricahua mountains (four specimens), the third unicuspid frequently is as large as the fourth. In southeastern Arizona, south of the Mogollon Plateau, there is a general yet pronounced tendency for the third unicuspid to be larger than the fourth or for both unicuspids to be of about the same size. However, to the north, in the San Francisco Peaks (three specimens) and Mogollon Plateau (47 specimens) region, the third unicuspid is markedly smaller than the fourth unicuspid in more than 95 per cent of the specimens.

Furthermore, specimens in the Grahams have slightly longer and broader skulls than specimens to the north, although the differences are slight and not consistent in other populations in southeastern Arizona. No color differences are evident between specimens from southeastern Arizona and central Arizona.

Although the differences shown in specimens from the Grahams, Huachucas, Chiricahuas, and Santa Ritas may be worthy of subspecific rank, for which the name *Sorex vagrans melanogenys* Hall is available, I consider these differences too minor and elect to employ the name *S. v. monticola.*

Specimens examined.—Hospital Flat, 2; Snow Flat, 2; 1/3 mi. W Columbine R.S., 1; Soldier Creek, 9400 ft., 1; Treasure Park, 1; Wet Canyon, 6000 ft., 2.

Myotis yumanensis yumanensis (H. Allen). Yuma myotis.—A single specimen of this species was taken as it flew across the road in Marijilda Canyon.

Specimen examined.—Marijilda Canyon campground, 1.

Myotis velifer brevis Vaughan. Cave myotis.—One specimen was shot flying over the pond, among pines and firs, late in the evening at Snow Flat, elevation 8750 feet, and another flying around the buildings at Bonita, elevation 4540 feet. The species undoubtedly occurs elsewhere between these elevations.

Specimens examined.—Bonita, 1; Snow Flat, 1.

Myotis evotis apache Hoffmeister and Krutzsch. Long-eared myotis.—After dusk, long-eared myotis were hanging separately along the center rafter in the boy scout building at Snow Flat. Never were more than two or three in sight at one time. At this same time, *Myotis velifer* and *M. volans* were flying over the pond adjacent to the building, for we shot bats of these two species, but not of *M. evotis,* over the pond. Apparently *M. evotis* does not feed until after it is much too dark to see to shoot bats. Long-eared myotis were not found in the scout building during the daytime.

Our specimens are a light reddish-brown above, ochraceous below. They are much more reddish than long-eared myotis from the San Francisco Mountains, Arizona.

Specimens examined.—Snow Flat, 4.

Myotis thysanodes thysanodes Miller. Fringe-tailed myotis.—A single specimen was obtained when it was caught in a bat net over the water tank at C N Ranch. It was associated with *Myotis californicus, M. volans, M. subulatus, Lasiurus borealis, Eptesicus fuscus,* and *Antrozous pallidus.*

Specimen examined.—C N Ranch, 1.

Myotis volans interior Miller. Hairy-winged myotis.—At Snow Flat, *M. volans* were flying and feeding over a pond with *Myotis velifer* and *Eptesicus fuscus.* Most specimens were taken high in the Mountains (8750 and 9400 feet), but some were taken much lower, as at C N Ranch (4900 feet) and Marijilda Canyon (4400 feet). In the ten specimens, there is considerable color variation on the dorsum: three are almost black, one a rich red, and the others varying degrees of ochraceous-tawny.

Specimens examined.—C N Ranch, 2; Marijilda Canyon campground, 1; Snow Flat, 6; 1/3 mi. W Columbine R.S., 1.

Myotis californicus californicus (Audubon and Bachman). California myotis.—This species flew over the chaparral at Marijilda and Stockton Pass and among the oaks over the water tank at C N Ranch. The species occurred below 5000 feet elevation except for Stockton Pass (5725 feet).

Specimens examined.—Stockton Pass, 1; C N Ranch, 1; Gillespie Wash, 1; Marijilda Canyon campground, 13.

Myotis subulatus melanorhinus (Merriam). Small-footed myotis.—Our specimens were taken among the oaks over a water tank at C N Ranch and among chaparral, oaks, and other trees at Stockton Pass campground.

Specimens examined.—Stockton Pass campground, 2; C N Ranch, 1.

Pipistrellus hesperus apus Elliot. Western pipistrelle.—Pipistrelles were encountered at numerous places near the base of the Mountains. They certainly must be one of the more common bats below 5500 feet elevation. They began feeding early in the evening, usually when it was still quite light, and fed relatively late in the morning. Pipistrelles were seen competing for food with violet-green swallows on several occasions (Van Gelder and Goodpaster, 1952) along the lower slopes of the Mountains. Some of the specimens are young of the summer, judging from the lack of fusion of the epiphyses.

Specimens from the Grahams are tentatively referred to the subspecies *P.h. apus* Elliot (Providentia mines, Sonora, Mexico). Our specimens seem too small to be referred to *P.h. maximus* (Dog Spring, New Mexico) or *P.h. santarosae* (Santa Rosa, New Mexico) and we suspect that pipistrelles in eastern Arizona, northern Sonora, and much of New Mexico are referrable to a race for which the name *P.h. apus* Elliot is available. Some average measurements, in millimeters, of our specimens are: 10♂, 9♀, total length, 71.6, 74.2; tail, 30.6, 32.3; hind foot, 6.2, 6.6; ear, 12.3, 12.6; forearm, 29.6, 30.9; greatest length of skull, 11.9, 12.2; breadth of braincase, 6.3, 6.4.

Specimens examined.—1 mi. NE Ft. Grant, 6; Pitchfork Ranch, 2; 2½ mi. S, 1 mi. E Maverick Mtn., 2; Gillespie Wash, 4; Jernigan Ranch, 5; 5 mi. SSW Pima, 1; 8 mi. SSW Pima, 4; Lebanon Reservoir No. 2, 3; Marijilda Canyon campground, 1.

Eptesicus fuscus pallidus Young. Big brown bat.—These bats were taken in numbers from the top to the bottom of the Mountains. At C N Ranch,

big browns were taken in a bat net over a water storage tank. In Wet Canyon, they were feeding very high, near the top of tall trees. At Snow Flat, they were shot while skimming across the pond. At C N Ranch, big browns were associated with red bats, pallid bats, California myotis, small-footed myotis, fringe-tailed myotis, and hairy-winged myotis; at Snow Flat, they were associated with cave myotis, hairy-winged myotis, and long-eared myotis. Big brown bats were much more abundant in the Grahams than they were farther south in the Huachuca Mountains. Seven specimens in our series of 38 do not have the epiphyses closed.

Color is variable in our specimens, some richly colored, others pale. This variation may occur within a series taken at one place on the same day, and seems not to be attributable to sexual or age differences. In size, our specimens are nearer to the measurements of bats from Escondido, San Diego County, California, called *E.f. pallidus* by Engels (1936) than to measurements of *E.f. bernardinus* from Tehama County, California.

Specimens examined.—76 Ranch, 1; Bonita, 2; C N Ranch, 9; Marijilda Canyon campground, 14; Wet Canyon, 2; Snow Flat, 7; 1/3 mi. W Columbine R.S., 2; Soldier Cr., 1.

Lasiurus borealis teliotis (H. Allen). Red bat.—Red bats were encountered flying over a water tank at the C. N. Ranch. One was taken August 13, 1952, in a bat net held over the tank. An adult female was shot two days later at the same place. The first specimen was a young female with the epiphyses of the fingers open. This animal may have been reared in the Grahams.

Specimens examined.—C N Ranch, 2.

Corynorhinus rafinesquii pallescens Miller. Western big-eared bat.—There is a single specimen of this subspecies in the collection of the U.S. Biological Surveys, labelled as Ash Creek, 4200 feet, Graham Mountains. The specimen was collected by Mr. E. G. Holt on June 21, 1914. We were unsuccessful in collecting bats of this species.

Antrozous pallidus pallidus (Le Conte). Pallid bat.—Pallid bats were numerous in the buildings at the Bird Farm, 6 mi. SSW Pima, in August, 1952, and from the accumulated droppings it was evident that at other times they had been far more abundant. Although efforts had been made to keep the bats out of the attics of the houses, many succeeded in getting in and others took refuge in the cracks in the wooden posts on the porches. Pallid bats prefer the lower slopes of the Mountains, but surprisingly the one at Stockton Pass was taken at 5725 feet, in an opening among oaks and junipers. Two pallid bats were caught in a bat net over the water tank at C N Ranch. Pallid bats at the Bird Farm were infested with the nycteribiid fly *Basilia antrozoi* Ferris.

Specimens examined.—Stockton Pass, 1; C N Ranch, 2; 6 mi. SSW Pima, 34.

Tadarida mexicana (Saussure). Mexican free-tailed bat.—Although no specimens of Mexican free-tailed bats were collected in the Grahams, bats with the characteristic flight of *Tadarida mexicana* were seen over a pond near Jernigan Ranch. Woodrow Goodpaster was confident they were *Tadarida*. Since he is familiar with this species elsewhere in Arizona, I have included it here.

These bats were flying very high and out of reach with a .410 shotgun. They flew almost as early as western pipistrelles.

Ursus americanus amblyceps Baird. Black bear.—Bears were quite common near the crest of the Mountains, and although they were not often seen, there was ample evidence of their presence. The bears usually were above 6500 feet, and probably came lower only when food was scarce. On Heliograph Peak, bears were feeding on Arizona thimble-berry, *Rubus neomexicanus,* in the summer of 1951. The residents at the Cluff Farm watched a bear turn over a log and feed on the insects beneath it. One bear wandered through the campground at Hospital Flat and another along our trap line at Soldier Creek in the summer of 1951. We had other reports the same summer of bears at Ladybug Saddle, along Ash Creek at Old Columbine, and at Turkey Flats.

Procyon lotor pallidus Merriam. Raccoon.—Raccoons occurred principally along the lower slopes, mostly between 4000 and 6500 feet and rarely high in the Mountains. A coon was seen running along the road 1/2 mi. SE Bonita, and footprints were seen in Taylor Canyon, 2 mi. N 76 Ranch; Ash Creek at Bird Farm; Wet Canyon, 6500 feet; and along Soldier Creek, near 9000 feet. The species was also reported at Angle Ranch, 5150 feet.

Goldman (1950) indicates *Procyon l. pallidus* Merriam occurs in the Gila River valley, but had no specimens from near the Grahams or the upper parts of the Gila River. Specimens listed by Goldman under *P. l. mexicanus* Baird occur as near the Grahams as do specimens listed under *pallidus.* It will be necessary to collect and study specimens from the Grahams to be certain of their subspecific status.

Nasua narica molaris Merriam. Coati.—Coatis or chulas are reportedly present now in the Grahams. However, they must be exceedingly scarce and may be recent immigrants. We saw none, but heard of a report that Earl Long, long-time resident and trapper in southeastern Arizona, saw "a band of about 15 at the north end of the Mountains." At a later date, March, 1953, Mr. Long wrote us that chulas are "present at this time in Graham Mountains." Mr. Long is a keen and competent observer, and we are inclined to give credence to his report. Through Steve Gallizioli, we learn that Charles Luster, state game ranger, saw 5 animals, judged to be coatis, cross the Swift Trail near Cyclone Hill in the summer of 1953.

Bassariscus astutus arizonensis Goldman. Ringtail.—Ringtails were fairly common in the lower parts of the Mountains. They frequently were encountered around buildings, for they are not shy at times. Ringtails reportedly were killed under the porch at the Cluff Farm and at the store at Bonita. One was caught in a garage at the Bird Farm in Ash Canyon. Mr. Steve Gallizioli has supplied us with some interesting notes on the one captured at the Bird Farm. A Say's phoebe was roosting on the front porch of the Gallizioli home at the Bird Farm in January, 1952. About 9:30 p.m., a ringtail came on the porch and jumped the phoebe, but got only the tail feathers. The phoebe frantically fluttered against the lighted window facing out onto the porch, but without hesitation the ringtail jumped again for the

bird. When the porch light was turned on, the cat ran up an apricot tree adjacent to the porch and over the roof of the house.

A ringtail, in all likelihood the same individual, was caught in a nearby garage. It took refuge there when the door of the garage was open and was entrapped when the door was closed. On February 3, a baited live trap caught the animal within a half an hour after being set at noon. For the three days that the animal was captive within the garage before it was caught in the trap, it had nothing to eat but the dried wings of some ducks stored in the garage. It had fed on these, for its droppings were filled with duck feathers. The ringtail was in considerable need of water after the three waterless days, and drank two-thirds of a pint in four hours. The ringtail was transferred to a larger cage inside the garage. On February 9, it escaped from the cage but forced its way into a live trap containing a wood rat by pushing the door inward and upward. On February 11, the animal again escaped from the cage within the garage but was retrapped February 16. On March 17 the ringtail was sent to the University of Illinois, Urbana, where it was kept alive until August, 1952. In captivity, the ringtail readily ate venison, hamburger, wood rat, kangaroo rat, *Peromyscus*, pocket gopher, black-tailed jack rabbit, white-crowned sparrow, house mice, bacon, canned dog and cat food, apples, and some fish. It ate cooked meat less readily than raw meat, and generally refused raw carrots. The ringtail usually devoured the entire mouse or rat, and most frequently started from the head. When a live animal was introduced, it was usually killed at once but if the ringtail was closely watched, or if there was no place to hide, it did not eat the animal until there was privacy. Only when the animal was being handled in a rough fashion—as when being transferred from one container to another—did it emit a musklike scent, but at this time the scent was strong and weasel-like in odor. Numerous efforts were made to tame the ringtail, but these met with little success.

The observations of this animal made at the Bird Farm were supplied by Steve Gallizioli, to whom we are indebted for the specimen and much of this information.

Specimen examined.—6 mi. SSW Pima, 1.

Spilogale putorius gracilis Merriam. Spotted skunk.—Spotted skunks must be rare in the Grahams, for we obtained none and heard few reports of their presence, whereas in the Huachucas they were common. However, there is an adult from the Grahams in the U. S. Biological Surveys collection, from 3200 feet, along Ash Creek. According to Steve Gallizioli, a trapper reportedly took "quite a number" of spotted skunks in North Taylor Canyon in 1949. A skunk caught at Angle Ranch and described to Richard Van Gelder seemed to fit the description of a *Spilogale*. The people at the ranch encountered this skunk in the chicken house, trying to kill a sick chicken.

Mephitis mephitis estor Merriam. Striped skunk.—We were unsuccessful in taking striped skunks in the Grahams, and we are of the impression that this species is uncommon. However, Earl Long writes us that the species is "plentiful." Steve Gallizioli reported to us that several striped skunks were killed by the fire guard at Webb Peak. Possibly these could have been hooded

skunks, *Mephitis macroura,* but *macroura* reportedly does not occur this far north in Arizona. A skunk had been killed at Bonita during the summer of 1951, and buried nearby. It was dug up, and the parts of the crushed skull that we recovered proved to be *Mephitis,* probably *M. mephitis.*

Conepatus mesoleucus venaticus Goldman. Hog-nosed skunk.—Hog-nosed skunks were numerous in the Mountains, especially above 6000 feet. Their rooting activities were harmful in the vegetable gardens at the Cluff Farm. Strychnined liver was put out at the farm one year, according to the Cluffs, and eight hog-nosed skunks were killed. Sign of this species of skunk was encountered at Snow Flat and the garbage pits near Turkey Flats. Steve Gallizioli found a hog-nosed skunk dead in the creek at Hospital Flat.

Our specimens differ to some extent from Goldman's description of *C. m. venaticus* in larger external size, slightly larger skulls, and absence of the "very" prominent sagittal crest in adult males.

Specimens examined.—Wet Canyon, 3; Cluff Farm, 2.

Taxidea taxus sonoriensis Goldman. Badger.—Badgers occurred all around the lower slopes of the Grahams. One taken near the C N Ranch had been feeding on insects and rock squirrels, judging from the stomach contents. A rock squirrel was used for trap-bait, and the remains in the stomach may have been this bait. The insects were of two species of scarabs, *Xyloryctes jamaicensis* (Drury) and *Strategus cessus* Le Conte. Numerous thorns of mesquite were found imbedded in the connective tissue beneath the skin of the badger. Only a few of the thorns were infected at the time, but probably all had been at some time. Although mesquite thorns are, by nature, very hard, those under the skin were soft and readily bent without breaking.

Near Ft. Grant, a badger successfully burrowed through the well-packed road.

Our specimens differ from *T. t. apache* Schantz in that they are not silvery in color and the dorsal median white line is not continuous to the tail. They seem to differ from *T. t. hallorani* in larger size and longer median white stripe. For the time being, we refer them to *T. t. sonoriensis.*

Specimens examined.—3 mi. S Fort Grant, 1; ½ mi. W C N Ranch, 1.

Mustela frenata neomexicana (Barber and Cockerell).—Long-tailed weasel. —At Soldier Creek Campground, 9350 feet, on August 23, 1952, Robert Calef saw an animal run across the trail from a boulder-covered hillside to some debris and rocks near Soldier Creek. He was confident the animal was a weasel, but he obtained only a brief glimpse of it. His description of the color of the animal's body as "honey brown" would be indicative of the pale coloration of *neomexicana.* Traps set around the spot where the animal disappeared caught nothing. We had no other reports of weasels, but Hall (1951b) records *Mustela f. neomexicana* from Safford and Sulphur Spring Valley. If the long-tailed weasel occurs in the Mountains, it would be of this subspecies.

Vulpes macrotis neomexicana Merriam. Kit fox.—On December 12, 1952, Steve Gallizioli found a kit fox, sex unknown, dead on U.S. Highway 666, 5 mi. S Safford. The specimen was badly mangled and only the tail was saved by Gallizioli. On March 6, 1953, he discovered a female kit fox, dead on

the road, approximately 12 mi. ENE Safford. Measurements of these two specimens, as taken by Gallizioli, are, respectively: Total length, 786, 797; tail, 318, 309; hind foot, 136, 127. The weight of the latter was 4 pounds, 4 ounces.

Kit foxes must be more numerous around the base of the Graham Mountains than around the Huachuca Mountains. In the Huachucas, we had absolutely no reports of kit foxes being present there for at least the past thirty years.

Urocyon cinereoargenteus scottii Mearns. Gray fox.—Gray foxes were not common in the Mountains in the summer of 1951 or 1952. One was seen jogging along the road 1 mi. S Heliograph Peak at 9 p.m., August 7, 1951, and two were seen in August, 1952, near the summit of Stockton Pass, one at 7:45 a.m. and one after dark. The latter 2 observations might have been of the same individual. Another gray fox apparently escaped from one of our steel traps along Noon Creek, 5200 feet, judging from the sign that remained. In March, 1953, Earl Long wrote us that gray foxes are "plentiful" in the Grahams. A trapper took numerous gray foxes in Ash Canyon during the winter 1951-1952, and our specimens are those taken by this trapper.

Specimens examined.—Ash Canyon, 6 mi. SSW Pima, 6 (skins only).

Canis latrans mearnsi Merriam. Coyote.—The coyote was scarce in the summer of 1952, but local residents attributed this to the effects of a recently completed 1080 poisoning campaign. In the summer of 1951 the coyotes did not seem to us to be any more abundant. On August 15, 1952, a coyote was heard barking by 5 p.m. at the Jernigan Ranch; at 5:30 p.m., a few days later, one was seen crossing the road 2 mi. SE Bonita.

Specimens examined.—Ash Canyon, 6 mi. SSW Pima, 2 (skins only, taken by trapper, winter 1951-1952).

Canis lupus baileyi Nelson and Goldman. Gray wolf.—Wolves have never been abundant in the Grahams, and are far less numerous than in the Huachucas. However, Dee Jernigan saw wolves on the southwest side of the Grahams in the winter of 1951-1952 and two wolves were taken in the Grahams during the "fiscal year" 1952-1953, according to Earl Long.

Felis concolor azteca Merriam. Mountain lion.—Mountain lions continue to persist in the Grahams despite persecution by the cattle raisers. In the southwestern part of the Grahams, one lion was present in 1952 and five in 1951, according to Dee Jernigan. Throughout the Mountains, seven were taken, according to Earl Long, from July, 1952, to March, 1953. These animals are said to do much damage to cattle. A lioness and two cubs supposedly killed 18 calves in the south end of the Mountains during one year in the late 1940's.

Specimen examined.—1½ mi. NW Cyclone Hill, 1 (skull only, pick-up).

Lynx rufus baileyi Merriam. Bobcat.—Bobcats are said to be present in considerable numbers along the lower slopes of the Mountains. However, we saw no sign of animals. A trapper working in Ash Canyon was successful in taking several in the winter of 1951-1952.

Specimens examined.—Ash Canyon, 6 mi. SSW Pima, 3 (skins only).

Ciltellus spilosoma canescens (Merriam). Spotted ground squirred.—These ground squirrels were abundant along the western base of the Mountains, particularly near Bonita. One favorite habitat was among the sacaton and in the tumbleweeds which had blown into the fences. In these situations, they were associated with *Sigmodon hispidus, S. minimus, Neotoma albigula, Sylvilagus audubonii, Dipodomys ordii, Perognathus penicillatus,* and *Peromyscus eremicus.* Along one fencerow, among an especially heavy tangle of tumbleweeds, several of the spotted ground squirrels caught in our rat traps were wet. We heard a snake going off through the weeds when we approached, and it seemed obvious that a snake had attempted to swallow the squirrels. In mid-August, half-grown squirrels outnumbered adults seen on the surface of the ground by about five to one.

Specimens examined.—76 Ranch, 1; 1½ mi. SW Ft. Grant, 4; 2 mi. NW Bonita, 3; ½ mi. NW Bonita, 7; Bonita, 1; 1/8 mi. SE Bonita, 3.

Citellus variegatus grammurus (Say). Rock squirrel.—Rock squirrels were common from the bottom to the top of the Mountains. They were seen below 4500 feet around the Bird Farm, at 4900 feet at the C N Ranch, at 5300 feet in the mouth of Taylor Canyon, at 5300, 6030, 7000, 7400, and 7500 feet along the Swift Trail Road, and at 9500 feet at the Columbine Ranger Station. At Columbine, rock squirrels were among firs and pines; at the Bird Farm, they were among mesquites and below the tree belt. In late August, some young were less than half grown at Columbine. At Turkey Flat, a young squirrel was captured alive. When we tried to photograph the animal, it escaped and, when pursued, readily climbed an oak to a point nearly 65 feet above ground.

At Cluff Farm, rock squirrels were said to do considerable damage to the vegetable plants.

Specimens examined.—C N Ranch, 1; 6 mi. SSW Pima, 1; Wet Canyon, 3; Cluff Ranch, 2; Soldier Creek, 1.

Citellus harrisii harrisii (Audubon and Bachman). Yuma antelope ground squirrel.—These ground squirrels occur on the lower slopes and the alluvial fans below 4500 feet elevation. They were numerous in 1951 along the east side of Stockton Pass. Here the squirrels were feeding on the fruits of the prickly pear cactus. Their forepaws and faces were stained from the juices, as were their intestinal tracts and muscles. The fruits of this cactus have many small, sharp spines, and one suspects that the squirrels must have suffered many times from the pricks of these spines. Price (in Allen, 1895) found these squirrels "On the cactus-covered plain (adjacent to the Grahams) . . . feeding on the seeds of the screw-pod mesquite, and one specimen shot had his cheek pouches distended with the shelled beans." One young of the year had nearly attained adult size by mid-August. *C. harrisii* was seen on the alluvial fan at the mouth of Taylor Canyon.

Specimens examined. — 2½ mi. S, 1 mi. E Maverick Mt., 2; 3 mi. S, 3 mi. E Maverick Mt., 1; Jernigan Ranch, 1; 8 mi. S, ½ mi. W Artesia, 3; Marijilda Canyon campground, 2; 1 mi. NW Cyclone Hill, 1; ½ mi. SW Cyclone Hill, 1.

Cynomys ludovicianus arizonensis Mearns. Black-tailed prairie dog.—A

large "dog town" was present at Bonita until it was poisoned off about 1918. Mearns (1907) writes that "For miles the burrows of these animals are thickly scattered over the plains south of the Pinaleno Range or Sierra Bonito, where the soil is clayey and better suited to the habits of this animal than the loose sand of most of Arizona." In the early settlement of the Sulphur Springs Valley, prairie dogs were so numerous that they were regarded as one of the greatest hindrances to successful farming and stock raising. Now, prairie dogs are entirely absent from within the area of this report.

Eutamias dorsalis dorsalis (Baird). Cliff chipmunk.—This chipmunk was numerous in many places among the pines and firs, especially where there were large boulders. They were also numerous among luxuriant stands of oaks, pines, and other trees found along some streams, as at 6000 feet along Wet Canyon. But it was a surprise to us to find this same species, *E. dorsalis*, among the sparse stands of juniper and chaparral at 4900 feet at the C N Ranch and at 5400 feet west of Angle Ranch. The habitats at the last two places are strikingly different from those at Wet Canyon or higher where chipmunks were present.

At the C N Ranch, cliff chipmunks were feeding, in August, on juniper berries and seeds of the squaw-bush. One chipmunk was watched here, foraging through a juniper and climbing as high as eight feet above the ground to select berries. Small branches were readily negotiated and frequently the chipmunk would jump nearly a foot from one branch to another. The animal gnawed on each berry for only a few seconds, then dropped it and reached for a new one.

Higher in the Mountains, chipmunks occurred along streams and in the forests of fir and pines. They were most often seen sunning themselves or chasing one another on rocks. At Snow Flat, a lactating female was shot in mid-August and on the next day at the same place, 3 young, less than half grown, were taken in mouse traps. These were apparently the offspring of the female previously collected. At Turkey Flat, a nest was found just beneath the bark of a dead pine. The nest was located 10 feet above the ground. Many pieces of cleansing tissue, salvaged from a nearby picnic ground, had been incorporated in the nest. In Wet Canyon, an adult chipmunk was shot on August 18 while carrying a small object in her mouth. This object proved to be a very young chipmunk (coll. no. 4975), with the eyes not yet open.

Chipmunks were seen, but not collected, at the following localities: South Taylor Canyon, 6000 feet; Shake Trail, a short distance above Stockton Pass (seen by Gallizioli); Ladybug Saddle; near Angle Ranch; Columbine Ranger Station; near Clark Peak; and Turkey Flat.

Specimens examined.—C N Ranch, 1; Wet Canyon, 2; Snow Flat, 7; Hospital Flat Forest Camp, 3; Hospital Flat, 1; Columbine R.S., 1; 1/3 mi. W Columbine R.S., 1; Soldier Creek, 1; 1 mi. E Clark Peak, 4; 2 mi. E Clark Peak, 1; 1½ mi. SE Clark Peak, 1.

Tamiasciurus hudsonicus grahamensis (Allen). Spruce squirrel.—The spruce squirrel or chickaree was not abundant anyplace in the Mountains. Wherever they were present, they did not chatter or bark as they did in places

where they were more common, as in the White Mountains to the north. We have a notion that this squirrel may have been more abundant at one time in the Grahams, but that the introduced Abert squirrel *(Sciurus aberti)* has occupied much of the habitat of *Tamiasciurus* and directly competes with it. Nearly all of the persons we talked with were unaware of the presence of the spruce squirrel in the Grahams, so uncommon are these squirrels now. In August, 1951, we found only one chickaree. This one, at Snow Flat, was in a large Douglas fir, and the ground beneath was littered with cuttings from cones. An Abert squirrel was present within 100 yards of the tree that the chickaree was in. In August, 1952, we saw more than a half-dozen chickarees, but were impressed with how secretive they were and the fact that they occupied the same woods as Abert squirrels.

In the late 1800's, Price (in Allen, 1895) found that in the Grahams this squirrel was "confined to the fir zone." Mearns (1907), under his account of the Arizona gray squirrel, *Sciurus arizonensis*, gives a March 21, 1889, reference of Edward D. Tuttle, clerk of Graham County, to the abundance of gray squirrels in the Grahams. This reference very well may have been to *Tamiasciurus;* we doubt that it was to *Sciurus arizonensis*. Steve Gallizioli reported chickarees to us in September, 1952, from Hospital Flat and 2 mi. E Columbine Ranger Station, and they are reportedly present on Grant Hill, 9400 feet.

Specimens examined.—Snow Flat, 1; Columbine Ranger Station, 2.

Sciurus aberti aberti Woodhouse. Abert squirrel or tuft-eared squirrel.—These squirrels occurred in the pine-fir forest from Turkey Flat on the southeast to near Clark Peak at the northwest. They were usually found above 7000 feet elevation, but, during the heavy snows of one winter, these squirrels reportedly came down the Mountains as low as Angle Ranch, 5150 feet.

Abert squirrels were "planted" in the Grahams by the Arizona Game and Fish Commission by 49 individuals trapped in October, 1941, and 20 in May, 1943, at Fort Valley, 10 miles north of Flagstaff. It is our belief that Abert squirrels did not occur in the Grahams before this "plant." They have done well since their introduction and probably have occupied much territory normally inhabited by the native spruce squirrel or chickaree, *Tamiasciurus hudsonicus grahamensis*. In the fall of 1951, only 11 Abert squirrels were reportedly taken during a limited hunting period of turkeys and squirrels. This small number is not indicative of their abundance, for Steve Gallizioli said that hunters avoided shooting at squirrels in order not to disturb the more prized game, the turkey.

Specimens examined.—Turkey Flat, 1; Snow Flat, 1; Columbine Ranger Station, 1; 1 mi. E Clark Peak, 1.

Thomomys in the Grahams.—Pocket gophers from high in the Graham Mountains are dark colored; those from the lower slopes—the lower edge of the oak belt and below—are reddish in color. In this respect, the gophers in the Grahams parallel those in the Huachuca Mountains and many other mountain ranges in Arizona, *i. e.*, those animals in the pine and fir forests are much darker than those on the lower slopes. As a matter of fact, we find it difficult or impossible to distinguish by color specimens of gophers taken

at 8800 feet elevation in the Huachucas from specimens taken between 8500 and 9500 feet in the Grahams, and the same is true for specimens taken at comparable lower elevations in the two mountain ranges. There are slight average differences in size which separate the races between the two mountain ranges, and it must be on these differences and not color that the separation is made. Some measurements, in millimeters, which demonstrate the slight morphological differences at comparable altitudes are:

	Total Length	Tail Length	Hind Foot	Basilar Length	Nasal Length
Grahams, 4500-5500 ft., 19 ♀♀	203.4	64.0	27.0	30.9	12.4
Huachucas, 4500-5500 ft., 29 ♀♀	198.4	67.3	28.4	30.7	12.1
Grahams, 8500-9500 ft., 35 ♂♂	223.9	66.3	29.9	33.9	13.9
Huachucas, 8500-9500 ft., 15 ♂♂	208.7	62.8	28.4	32.3	12.9

Specimens of gophers from high in the Huachuca Mountains (above 8500 feet) have been referred to the species *Thomomys umbrinus* by many workers (one of the latest, Goldman, 1947). Because of the close similarity between those in the Huachucas and those in the Grahams, the dark-colored gophers from the Grahams might be referred to *Thomomys umbrinus* also. As a matter of fact, one specimen from Soldier Creek, in the Grahams, had only three pairs of mammary glands, a supposedly diagnostic feature of *T. umbrinus*. However, five other specimens from the same place had four pairs, supposedly typical of the condition in *Thomomys bottae*. The specimen with three pairs is in morphological and color features the same as those with four pairs. There seems to be no basis for referring our material to *T. umbrinus*. Hoffmeister and Goodpaster (1954) concluded that no specimens from the Huachucas were referable to *T. umbrinus*, and questioned the occurrence of this species in Arizona. All of our specimens from the Grahams are referred to the earlier named *T. bottae*.

In the Grahams, it is possible to go from about 4000 feet to 10,000 feet in a distance of a few miles. Pocket gophers are to be found at many places between these extremes in altitude. We were interested to see how size of pocket gophers in the Grahams might correlate with variations in altitude. Davis (1938) in working with gophers in Idaho points out that "If one compare individuals from poorer soils (for pocket gophers) with others from progressively better and deeper ones, the size of both sexes is found generally to increase, males more so than females." Davis found that the progressive reduction in size was up the mountain, with the smallest individuals on the average at higher altitudes. We find the reverse to be true, with the larger gophers high, the smaller, low in the Grahams. Near the top of the Mountains they are largest in external features, skull measurements, and the overall size of the skull (assuming that the product of skull-length, zygomatic breadth, and palatofrontal depth gives such a measure). Table 1 indicates the progressive increase in average size with increasing altitude. Although the relationship of size to altitude in the Grahams is the reverse of what Davis (1938) found to be the case, his correlation between large size and better soil probably is the most significant. To us, it seems apparent that the soil in the high mountain

TABLE 1.—Pocket gophers from different elevations in the Graham Mountains

Elevations	Number of specimens	Total length	Tail length	Hind foot length	Ear length	Product: Basilar x zygomatic x palato-frontal	Basilar length	Zygomatic breadth
				Males				
4500-5000 ft.	6	209.8	71.7	29.5	6.7	8786.1	31.1	21.9
5000-5500 ft.	4	216.8	72.0	29.3	6.8	9860.9	31.9	22.4
7000-8000 ft.	3	220.5	71.5	31.0	7.3	11480.5	33.5	23.0
8500-9500 ft.	35	223.9	66.3	29.9	6.6	11910.1	33.9	23.9
				Females				
4500-5000 ft.	14	203.1	63.8	27.2	6.2	9203.1	31.1	21.6
5000-5500 ft.	5	203.6	64.6	26.6	6.8	8335.5	30.3	21.0
7000-8000 ft.	6	206.0	59.8	27.5	6.7	9913.3	31.8	21.8
8500-9500 ft.	46	212.4	65.5	28.4	6.3	9985.3	31.9	22.2

	Mastoid breadth	Nasals length	Interorbital breadth	Diastema	Rostrum length	Rostrum breadth	Palatilar length	Palatofrontal depth
			Males					
4500-5000 ft.	18.7	12.7	6.4	12.2	15.0	7.5	20.7	12.9
5000-5500 ft.	18.6	13.0	6.5	12.6	15.3	7.7	21.8	13.8
7000-8000 ft.	20.3	14.8	7.0	13.4	17.2	8.2	22.7	14.9
8500-9500 ft.	19.5	13.9	6.8	13.6	16.8	8.0	23.4	14.7
			Females					
4500-5000 ft.	18.6	12.4	6.6	12.1	14.7	7.4	21.1	13.6
5000-5500 ft.	18.1	12.5	6.3	11.8	14.7	7.3	20.5	13.1
7000-8000 ft.	18.6	13.6	7.0	12.6	15.8	7.8	21.2	14.3
8500-9500 ft.	18.7	13.1	6.7	12.4	15.6	7.5	21.6	14.1

meadows, above 8500 feet elevation in the Grahams, is deeper, less rocky, and far more easily dug through (by our hands or trowels) than soil on the desert, as near Ft. Grant, Jernigan Ranch, or C N Ranch. Martin and Fletcher (1943), in studying the soils of the Grahams, point out that the soils of the high mountain meadows are mellow and granular, varying in thickness from twelve to seventeen inches, and their profiles are typical of prairie soils. Furthermore, and most significantly, the subsoil to a depth of twenty to thirty-six inches is structurally similar to the surface horizon. In the oak-woodland in the Grahams, a cloddy substrate is encountered below a layer about fourteen inches thick. This substrate must be less suitable to gophers than that of the mountain meadows. In desert-grassland and desert areas, this cloddy substrate may even be nearer the surface. It would appear from Martin and Fletcher's report that the soil would be more friable to a greater

depth and thus more suitable for gophers in the high meadows. Gophers were certainly more abundant there than anywhere else in the Mountains.

In August, eighty-six sexually mature female gophers were saved as skins, but none has an indication on the label that it contained embryos. Five are listed as lactating, and all of these are from high in the Mountains.

Thomomys bottae grahamensis Goldman. Western pocket gopher.— Gophers taken above 6000 feet elevation in the Grahams are noticeably darker than those taken at lower elevations. In these specimens, the fur of the back is heavily mixed with blackish hairs. Specimens from Noon Creek, at 5450 feet elevation, are somewhat intermediate in coloration between those of the lower slopes and higher slopes, but appear to be nearer those from high in the Mountains.

Pocket gophers of this subspecies inhabited the mountain meadows grown up with perennial grasses and sneeze-weed *(Helenium hoopesii)*. The meadows were surrounded by white fir, Douglas fir, and yellow and limber pines. Gophers were exceedingly numerous in these meadows. That they were active in the winter as well as in the summer was indicated by the presence of earth cores left on the surface of the ground after the snow had melted.

At Wet Canyon, gophers were taken along a creek among alders, maples, oaks, and pines where there was very little grass. At Turkey Flat, they inhabited gently sloping ground grown up with bracken. Gophers, presumably of this subspecies, were present in small numbers at the very top of Webb Peak, 10,000 feet elevation.

Specimens examined.—Noon Creek, 2; Wet Canyon, 4; Turkey Flat, 12; Snow Flat, 6; Treasure Park, 32; Hospital Flat, 11; Soldier Creek, 20; Soldier Creek campground, 1; head Soldier Creek, 15; Columbine R.S., 2; 1/3 mi. W Columbine R.S., 11; 6 mi. W Columbine R.S., 1; Goudy Creek Canyon, 2; Chesley Flat. 6.

Thomomys bottae extenuatus Goldman. Western pocket gopher.—Pocket gophers at elevations below 5400 feet in the Grahams are rather uniformly bright cinnamon buff in color. Those at the northern end of the Mountains (as at the Bird Farm) are similar in color to those from near the southern end (as near Jernigan Ranch). The same is true for specimens from the east and west sides of the Mountains below 5400 feet. All of these specimens are referred to the race *T. b. extenuatus*. Goldman (1947) indicates that specimens from along the Gila River are referable to *T. b. alienus*, but specimens from Bird Farm, six miles from the Gila, seem no different from those referred to *T. b. extenuatus* from much farther south. Specimens of gophers referable to *Thomomys baileyi mearnsi* have been taken from the Sulphur Springs Valley near Willcox, according to Goldman (1947). However, none of our specimens from the Grahams seems to be of this species.

Specimens of this subspecies were taken among mesquite, yucca, cactus, and catclaw at most localities. Near Fort Grant, they lived among beardgrass *(Andropogon)*; at Jernigan Ranch, among beargrass *(Nolina microcarpa)*, agave, and catclaw; near CN Ranch, among the oaks; at Angle Ranch, among the grass growing in an orchard.

Specimens examined.—1½ mi. SW Ft. Grant, 12; Stockton Pass campground, 4; CN Ranch, 4; ½ mi. W CN Ranch, 5; Jernigan Ranch, 4; 6 mi. SSW Pima, 3; Marijilda Canyon campground, 2; Angle Ranch, 9.

Perognathus flavus flavus Baird. Silky pocket mouse.—Silky pocket mice were not common in any of the places we collected. At 3/4 mi. SE Bonita, one specimen was taken in a patch of high, green weeds which resembled lambs quarters. At the Bird Farm, 6 mi. SSW Pima, the single specimen collected was running on damp ground beneath some cottonwoods. The one female collected on August 29 had four embryos. Our specimens do not differ appreciably in color from specimens from the Huachuca Mountains.

Specimens examined.—1½ mi. SW Ft. Grant, 2; Bonita, 1; 1/8 mi. E Bonita, 1; 3/4 mi. SE Bonita, 1; 8 mi. S, ½ mi. W Artesia, 1; 6 mi. SSW Pima, 1.

Perognathus baileyi baileyi Merriam. Bailey pocket mouse.—At the Bird Farm, 6 mi. SSW Pima, both *Perognathus baileyi* and *P. penicillatus* were taken in the same short trap-line. Little difference in habitats between the 2 species could be noted, but *P. baileyi* was taken more frequently among dense growths of tumbleweeds. Along the western base of the Grahams, as at the 76 Ranch, *P. baileyi* was trapped among much mesquite, some rocks, and little grass. Near Maverick Mountain, these pocket mice were taken among mesquite, prickly pear cactus, yucca, and some agave.

Specimens examined.—76 Ranch, 1; 2½ mi. S, 1 mi. E Maverick Mtn., 7; 6 mi. SSW Pima, 3.

Perognathus penicillatus pricei Allen. Desert pocket mouse.—*Perognathus penicillatus* was taken in a variety of habitats, but it occurred most commonly where there was sparse, short grass, mesquite, and some cacti. At the Bird Farm, *P. penicillatus* was found with *Perognathus baileyi*. In August, we took all sizes of *Perognathus penicillatus*, from young still in the nest to adults. Approximately one-fifth of those collected were juveniles or sub-adults. Two young, with eyes unopened, were dug out of a nest on August 19 by Charles McLaughlin when exploring for gophers at the Bird Farm. The nest was about 12 inches below the surface of the ground, ball-like in nature, and consisted of less than a cup of dry grass. The young were completely, but sparsely, haired. Of 27 mature females, none had embryos in August, although some were lactating. The breeding season for *Perognathus penicillatus* may be over by the first part of August.

A mite removed from a desert pocket mouse near Ft. Grant was of the genus *Androlaelops*.

Specimens examined.—76 Ranch, 1; Haunted Ranch, 6; 1/3 mi. SE Ft. Grant, 5; 1½ mi. SW Ft. Grant, 15; ½ mi. NW Bonita, 4; 3 mi. S Ft. Grant, 5; 3/4 mi. SE Bonita, 4; 2½ mi. S, 1 mi. E Maverick Mtn., 1; 8 mi. S, ½ mi. W Artesia, 2; 6 mi. SSW Pima, 50; Marijilda Canyon campground, 1; 1/4 mi. S Cyclone Hill, 1.

Diplodomys ordii ordii Woodhouse. Ord kangaroo rat.—*D. ordii* was far less common than *D. merriami*. Most specimens were taken between Ft. Grant and Bonita. This species lived in much the same habitat as *Onychomys leucogaster* and was usually taken on the open flats among yucca, mesquite, cacti, and some grasses. One, out of 11 mature females, had 4 embryos.

Specimens examined.—76 Ranch, 1; 1½ mi. SW Ft. Grant, 12; ½ mi. NW Bonita, 2; 1/8 mi. E Bonita, 1; 3/4 mi. SE Bonita, 3; 3 mi. S Ft. Grant, 2; 2 mi. S, 3 mi. E Maverick Mtn., 1.

Dipodomys spectabilis spectabilis Merriam. Banner-tailed kangaroo rat.—Banner-tailed kangaroo rats were encountered on the southwestern side of the

Grahams only. Their mounds were most evident along the Stockton Pass road about a mile east of Bonita. The elevation was approximately 4600 feet. These "dipos" were taken in steel traps. Although we usually have caught only one banner-tailed kangaroo rat from one mound during a trapping period, two were caught from one mound on the same night near Bonita.

These specimens are from within 35 miles of the type locality of *D. s. spectabilis*. All are adults and molting.

Specimens examined.—2 mi. NW Bonita, 3; 3 mi. E Bonita, 2.

Dipodomys merriami merriami Mearns. Merriam kangaroo rat.—"Dipos," of this species, were exceedingly abundant at the Bird Farm, 6 mi. SSW Pima. They were in the sandy areas among grasses, snake-weed, tumbleweeds, cholla, mesquite, and other bushes. At the Bird Farm it was usually possible to see a half-dozen "dipos" when running a trap-line after dark. The rats did not seem to be attracted to our traps by the oatmeal bait, for frequently we watched them hop around the trap without once taking any of the oats. Some "dipos" were caught in a net improvised by Charles McLaughlin and one was caught in a gopher trap set below ground for a *Thomomys*. Individuals of *D. merriami* at the Bird Farm were observed to show antagonism toward one another on at least one occasion. For example, two kangaroo rats were seen to meet face to face and run quickly in a circular fashion as if jockeying for position and preparing to spar. Facing each other all the time, each gave a squeak, then each jumped back, and they continued on their respective ways.

D. merriami occurred at all of the places that *D. ordii* was taken, and in addition in numerous other places. We could note no differences in ecological preference where the two were taken together.

In August, six of thirty-five mature females were pregnant, of which four contained three embryos and two contained only two embryos. One female was lactating. Two of our specimens are quite small, and apparently were born early in the summer. One would suspect that these kangaroo rats have at least two litters each summer—perhaps one in June and another in early September.

Specimens examined.—Haunted Ranch, 2; 1/3 mi. SE Ft. Grant, 3; 1½ mi. SW Ft. Grant, 4; 2 mi. NW Bonita, 1; 3 mi. S Ft. Grant, 6; 2 mi. E Bonita, 1; 3½ mi. E Bonita, 1; 4 mi. E Bonita, 1; 2½ mi. S, 1 mi. E Maverick Mtn., 16; 3 mi. S, 3 mi. E Maverick Mtn., 1; 2½ mi. SW Artesia, 2; 4 mi. S Artesia, 1; 7½ mi. S, 2 mi. W Artesia, 1; 8 mi. S, ½ mi. W Artesia, 14; 6 mi. SSW Pima, 24; ½ mi. SW Cyclone Hill, 1.

Castor canadensis subsp. Beaver.—A house, cuttings, and a few small dams of beavers were seen along Soldier Creek, 1/3 mile due west of Columbine Ranger Station. The house was unoccupied in August, 1952. The flow of water in Soldier Creek is small and this stream could not provide refuge for many beavers at any time. We had oral reports of sign of beavers on some other creeks, but did not verify these. Beavers were planted in the Grahams by the Arizona Game and Fish Commission, for "four animals were trapped in the White Mountains and released in the Grahams, on August 24, 1950," according to Wendell Swank (letter of March 27, 1953). Swank points out that releases in the Mountains may have been made before this

date, but the state has no record of any such releases. Because of the small amount of water in any of the creeks in the Grahams, it is questionable if beavers occurred naturally in the Mountains.

It is not possible to be certain of the subspecific identity of the beavers transplanted from the White Mountains, for they, in turn, probably came from still another place.

Onychomys leucogaster ruidosae Stone and Rehn. Northern grasshopper mouse.—*Onychomys leucogaster* was taken at only three localities, and at two of these localities in association with *O. torridus*. *O. leucogaster* seems to prefer more open situations than *O. torridus*, but no marked differences in habitat preferences could be discerned by us. Near Fort Grant, northern grasshopper mice occurred on the flats where there was some yucca and mesquite, intermixed with a small amount of grasses and sacaton. Near Bonita, *O. leucogaster* was taken along a fence where there was little cover but numerous holes.

We found it even more difficult in the field to distinguish between *O. leucogaster* and *O. torridus* in the Grahams than in the Huachucas. This was especially true for juveniles and subadults. The proportionate length of the tail (less than half the body in *leucogaster*) served in about 90 per cent of the specimens. In cleaned skulls, length of maxillary toothrow always served to distinguish between the two species (alveolar length always 4.4 mm. or more in *leucogaster*, always 4.3 or less in *torridus*).

Specimens examined.—1½ mi. SW Ft. Grant, 14; Bonita, 2; ¾ mi. SE Bonita, 1; ⅛ mi. E Bonita, 1.

Onychomys torridus torridus (Coues). Southern grasshopper mouse.—*O. torridus* was frequently taken in or near tangles of tumbleweeds. In some places it was found in heavy stands of sacaton. At the Bird Farm, the species was closely associated with *Perognathus baileyi*, *P. penicillatus*, *Dipodomys merriami*, *Sigmodon hispidus*, and *Thomomys bottae*. At two places, 1½ mi. SW Ft. Grant and ¾ mi. SE Bonita, this species was associated with *O. leucogaster*. We have the impression that *O. torridus* occurs in much the same habitat as *Dipodomys merriami*.

Although many of our specimens were taken near Fort Grant, Graham County, this locality is not to be confused with the type locality of the subspecies—"*Camp* Grant." Prior to 1872, Camp Grant, sometimes called Fort Grant, was located "on the San Pedro River at junction with Arivaipa creek" (see Barnes, 1935). The type specimen of *Onychomys torridus torridus* was collected in 1867 by Edward Palmer. Fort Grant was not transferred to its present location at the west base of the Graham Mountains until 1872, according to Barnes. Therefore, the type locality would have been along the San Pedro River, at Arivaipa Creek, 47 miles northwest of the present Fort Grant, or two miles south of Feldman, in Pinal County.

Specimens examined.—1½ mi. SW Ft. Grant, 3; ½ mi. NW Bonita, 4; ¾ mi. SE Bonita, 6; 8 mi. S, ½ mi. W Artesia, 1; 6 mi. SSW Pima, 10; ¼ mi. S Cyclone Hill, 1.

Reithrodontomys megalotis megalotis (Baird). Western harvest mouse.—Harvest mice of this species have been taken high in the Grahams (9000 feet or

above) and again near the base (4700 feet or lower). Those mice from high in the Mountains were taken at Soldier Creek and at Hospital Flat. At these places the mice were closely associated with *Microtus longicaudus, Sorex vagrans,* and *Peromyscus maniculatus rufinus.* At Soldier Creek they lived among grass that in many places was three feet high, with the ground nearly always damp and frequently with standing water. At Hospital Flat, a mouse was taken in thick grass 14 to 18 inches tall alongside a trickle of water. On two previous nights no mammals were trapped here; on the third night, the one *Reithrodontomys* was caught.

Near the base of the Mountains, harvest mice were taken in association with *Dipodomys, Onychomys,* and *Peromyscus eremicus.* Mice from the vicinity of Bonita and Ft. Grant were taken between 4500 feet and 4700 feet. In some places, they were caught where the vegetation was sparse, with some tumbleweeds, sunflowers, and other weeds. At other places, they lived among sacaton and grama, with some mesquite and yucca.

Those mice from the "top" of the Mountains lived in a habitat so different from that at the bottom of the Mountains, that we suspected two subspecies might be represented in our specimens. Such is the case in *Peromyscus maniculatus.* However, we cannot discern any differences in the populations of *Reithrodontomys megalotis* so widely separated altitudinally. The variation in color within the group of adults from the base is much greater than it is between mice from the top and bottom. At one time we suspected that those harvest mice living high in the mountains of southeastern Arizona might be referable to *Reithrodontomys megalotis arizonensis,* for it was described from 8000 feet in the Chiricahua Mountains and is said to be darker and more ochraceous (perhaps parallel to the darker color in the mountain-inhabiting *Peromyscus maniculatus rufinus).* Our specimens from high in the Grahams are not noticeably darker or more ochraceous, and we have not referred them to *R. m. arizonensis.*

Specimens examined.—1½ mi. SW Ft. Grant, 15; ½ mi. NW Bonita, 2; ⅛ mi. NE Bonita, 2; Bonita, 1; ¾ mi. SE Bonita, 3; Hospital Flat, 1; Soldier Creek, 4.

Baiomys taylori ater Blossom and Burt. Pigmy mouse.—One specimen of the pigmy mouse, *Baiomys taylori,* was obtained in the Graham Mountains. This record is the most northern one in the United States, and 80 miles north of the previously recorded occurrence in the Huachuca Mountains. The specimen, a female, has the following measurements: total length, 113; tail, 48; hind foot, 14; ear, 12.

Our specimen was taken in a habitat of mesquite, sacaton, yucca, grama, and some other low bushes. In particular, it was trapped alongside a bunch of sacaton. Not until the third night that traps had been set at this locality was the mouse taken. At least 250 traps were set on four successive nights in the same habitat and at the same general locality where the *Baiomys* was taken, but no other pigmy mice were caught. In the immediate area from which the *Baiomys* was trapped, we caught *Sigmodon hispidus, Reithrodontomys megalotis, Onychomys leucogaster,* and *Onychomys torridus.*

Specimen examined.—1½ mi. SW Ft. Grant, 1.

Peromyscus maniculatus sonoriensis (LeConte). Deer mouse.—Two specimens of *Peromyscus maniculatus*, taken along the western base of the Mountains, below 4650 feet, are markedly lighter than specimens of *P. maniculatus* taken higher in the Mountains. Because of their coloration, we refer them to *P. m. sonoriensis.*

Peromyscus maniculatus was next encountered at 8750 feet, and then from this altitude up to the highest place we trapped (10,000 feet on Webb Peak). There must be a zone between 4700 and 8700 feet where *Peromyscus maniculatus* is scarce or absent. This zone is probably an important barrier between the two subspecies, *P. m. sonoriensis* and *P. m. rufinus.*

The specimen taken near Bonita was trapped among tumbleweeds, sunflowers, mesquite, and sacaton.

Specimens examined.—1½ mi. SW Ft. Grant, 1; ¾ mi. SE Bonita, 1.

Peromyscus maniculatus rufinus (Merriam). Deer mouse.—Deer mice inhabited the conifers adjacent to grassy meadows, but occasionally they were taken in the meadows themselves. They were in association with *Sorex vagrans, Reithrodontomys megalotis,* and *Microtus longicaudus. Peromyscus boylii* seemed to occur farther away from the grassy meadows than did *P. maniculatus rufinus.* As a result, *P. boylii* and *P. maniculatus* were rarely found even closely associated. On the top of Webb Peak, deer mice were taken in heavy woods, but no *P. boylii* were taken here. This may be too high, altitudinally, for *P. boylii.*

In August, 6 females were pregnant, one with 3, two with 4, two with 5, and one with 6 embryos. Three other females were lactating. Most of the specimens trapped during this month were immatures.

Specimens examined.—Snow Flat, 11; Hospital Flat, 4; Hospital Flat Forest Camp, 2; Columbine Ranger Station, 10; 1/3 mi. W Columbine R.S., 8; Soldier Creek, 42; head Soldier Creek, 3; Webb Peak, 11; Chesley Flat, 4; Goudy Canyon, 2.

Peromyscus leucopus ochraceus Osgood. White-footed mouse.—Only along the west base of the Mountains, among cactus, mesquite, yucca, and sparse grasses, were we able to catch *Peromyscus leucopus.* Associated with this species were *P. eremicus, P. maniculatus, Onychomys leucogaster, O. torridus, Dipodomys ordii,* and *D. merriami.*

One of our specimens is an adult; the others are subadults or young. This adult seems more Ochraceous-Buff than specimens of *P. l. arizonae,* and in this respect resembles *P. l. ochraceus.* The upperparts seem to be more heavily overlaid with dusky than is ascribed to *P. l. ochraceus.* All six of our specimens apparently are intergrades between *arizonae* and *ochraceus,* and until more material is available, we tentatively regard them as nearer to *P. l. ochraceus.*

Specimens examined.—1½ mi. SW Fort Grant, 6.

Peromyscus boylii rowleyi (Allen). Brush mouse.—The brush mouse was common in the oak belt between 5300 and 8900 feet. It was less common near the crest of the Mountains and absent from the top of Webb Peak

(10,000 feet). Seven females collected in August were pregnant, of which five had 2 embryos each and two had 4 embryos.

Specimens examined.—Pitchfork Ranch, 1; Stockton Pass campground, 1; Angle Ranch, 5; Noon Creek, 8; Wet Canyon, 19; Turkey Flat, 3; 2/5 mi. S Heliograph Peak, 10; 1 mi. S Heliograph Peak, 11; Hospital Flat, 1; 1/3 mi. W Columbine R. S., 1; Soldier Creek, 3.

Peromyscus eremicus eremicus (Baird). Cactus mouse.—This species lived on the flats and alluvial fans and below the wooded portions of the Grahams. It was frequently found associated with *Perognathus penicillatus*. Young, only a few weeks old, and adults were trapped in August. Two females contained 3 embryos each in this month.

Osgood (1909) indicates on his range map that *P. e. anthonyi* might be expected in the Grahams, but lists specimens from Ft. Grant under *P. e. eremicus*. The subspecific status of *P. eremicus* in southeastern Arizona should be reviewed.

Specimens examined.—1½ mi. SW Ft. Grant, 14; ½ mi. NW Bonita, 3; ¾ mi. SE Bonita, 6; 3 mi. S Ft. Grant, 2; 2½ mi. S, 1 mi. E Maverick Mtn., 1; 6 mi. SSW Pima, 11; Marijilda Canyon campground, 2; ¼ mi. SW Cyclone Hill, 1.

Sigmodon hispidus confinis Goldman. Hispid cotton rat.—*Sigmodon hispidus* lived in a thicket of green and dead tumbleweeds near a reservoir at the Bird Farm. They were also found in an area grown up with sacaton, prickly poppy, mesquite, yucca, and a small amount of grama grass at 1½ mi. SW Ft. Grant. *Sigmodon minimus* was taken in this same situation, but *S. hispidus* was more abundant. Down the road, near Bonita, the two species of cotton rats also occurred together, but *S. minimus* was more abundant there. Hall and Davis (1934) noted that Annie Alexander found both species together at Ft. Grant in 1933.

Hall and Davis (*op. cit.*) regarded specimens from Fort Frant as referable to *S. h. cienegae* rather than to *S. h. confinis*. All localities within the Graham Mountains are within 25 miles of the type locality of *confinis* (Safford, Arizona) and much farther removed from the type locality of *cienegae* (near Fort Lowell, Arizona). Our specimens from Fort Grant on the southwest side of the Mountains are no different from specimens from the Bird Farm, on the northeast side. Those from the Bird Farm are within 10 miles of Safford. Furthermore, in those features judged to be of greatest diagnostic value, especially length of hind foot, all of our specimens seem to be nearer to *S. h. confinis*. Features of size, however, may not be too reliable for we think that *Sigmodon* continues to grow throughout much of its lifetime. For example, in five specimens of *Sigmodon minimus* all of which might be regarded as adults, judging from pelage, total length varies thus: 198, 225, 233, 202+, 247; corresponding nasal-length: 10.3, 12.1, 12.0, 11.8, 12.8; corresponding greatest lengths of skull, 29.3, 31.3, 32.6, —, 33.9. I believe that length of parts have significance only when *Sigmodon* of comparable ages are employed.

Specimens examined.—1½ mi. SW Ft. Grant, 4; ⅛ mi. SE Bonita, 1; Bonita, 1; 6 mi. SSW Pima, 4.

Sigmodon minimus minimus Mearns. Least cotton rat.—Near Bonita, this species inhabited a thick patch of sacaton which grew profusely between the road and fence. There was ample sign of cut grass around the clumps of sacaton. Some of these cuttings may have been made by cottontails, which were present there, but the majority must have been made by cotton rats. In this patch of grass there were many kinds of mammals, including *Citellus spilosoma, Neotoma albigula, Reithrodontomys megalotis, Peromyscus eremicus, P. maniculatus, Perognathus penicillatus, Onychomys, Sigmodon hispidus, Sylvilagus audubonii,* and *Lepus californicus.* Adult and immature *Sigmodon minimus* were taken during both the daytime and nighttime.

It is quite easy to tell the skins of *S. minimus* and *S. hispidus* apart, but it is difficult to make an easy differentiation of the skulls in the two species. In the Grahams, the skulls of *minimus* differ from those of *hispidus* usually in the following features: alveolar length of upper molars less than 6.5 mm in *minimus,* instead of 6.5 mm or more when the molars show some wear; posterior palatal spine bounded laterally with deep palatal pits in *minimus* rather than with shallow pits or no pits.

We can find no differences between our specimens from the Grahams and *S. minimus* from the Huachucas, and refer our specimens to *S. m. minimus.* They are not as dark as *S. m. woodi.*

Specimens examined.—½ mi. NW Bonita, 2; Bonita, 3; ¾ mi. SE Bonita, 1.

Neotoma albigula albigula Hartley. White-throated wood rat.—White-throated wood rats were collected at elevations below 5200 feet. The tangles or thickets of tumbleweeds accumulated along fencerows and around large mesquites provided good cover for these rats. They constructed well-made runs through the tumbleweeds. At the Bird Farm, a black-tailed rattlesnake (*Crolatus molossus*) and a white-throated wood rat were taken on successive days from holes about two feet apart beneath the same mesquite.

At several places, these wood rats had been feeding on the red fruits of the prickly pear cactus. In such cases, it was found that most of the soft anatomy of the rats was stained a reddish pink from these fruits. This even extended to the muscles of the legs, and the urine was exceedingly bright colored.

In August, two females had embryos and two others were lactating. No females of *Neotoma mexicana,* taken the same month but higher in the Mountains, were pregnant or lactating.

Specimens examined.—1½ mi. SW Ft. Grant, 1; ½ mi. NW Bonita, 5; Bonita, 3; ¾ mi. SE Bonita, 1; 3 mi. S Ft. Grant, 3; 6 mi. SSW Pima, 6; ¼ mi. S Cyclone Hill, 10; Angle Ranch, 3.

Neotoma mexicana mexicana Baird. Mexican wood rat.—This species usually lived above 8700 feet in the Grahams. At Hospital Flat, they inhabited a heavy stand of pines and firs. One rat had a nest inside a hollow tree, but at its base. On Heliograph Peak, *Neotoma mexicana* was encountered living in a drier, warmer situation, with pines, locust, scrubby bushes, and rocks.

The Graham Mountains are situated geographically between the ranges

of three named subspecies of *Neotoma mexicana* (see Goldman, 1910): *mexicana, bullata,* and *pinetorum*. Hoffmeister and Goodpaster (1954) do not regard the race *N. m. bullata* as distinct from *N. m. mexicana*. Our thirteen adult specimens from the Grahams seem clearly referable to *N. m. mexicana*. They are smaller externally than *N. m. pinetorum,* and the basilar length and zygomatic breadth is less. The auditory bullae are about the same size as that characteristic of *mexicana,* less inflated than in *pinetorum*.

Specimens examined.—2/5 mi. S Heliograph Peak, 5; 1 mi. S Heliograph Peak, 7; Snow Flat, 1; Hospital Flat, 1; 1/3 mi. W Columbine Ranger Station, 1; Soldier Creek, 2; Goudy Canyon, 2; Ash Creek, 6100 to 9200 ft., 6 (U.S. Biol. Surv. Coll.).

Microtus longicaudus leucophaeus (Allen). Long-tailed vole.—*M. l. leucophaeus* can be found in any of the meadows or flats in the Grahams above 8000 feet, where the grass is tall and thick and becomes heavily saturated with dew during the summer nights. In such meadows, there is usually one or several small trickles of water, and since the grass is usually thicker around these places, long-tailed voles are most frequently trapped there. The voles may make well-constructed or much-worn runways in some places, but not in others. The voles may be present, and even abundant, although little or no grass cuttings are evident along the runways. Frequently, there was standing water among the grass where they lived. In some places, it was profitable to set our traps in likely-looking spots so near creeks that a slight increase in the flow of water caused the traps to float away. Associated with long-tailed voles in these damp meadows were *Sorex vagrans* and *Reithrodontomys megalotis*.

In some places, *M. l. leucophaeus* invaded the coniferous woods surrounding the meadows. This was particularly true near Chesley Flat. In one place, a specimen was taken in a more arid and different situation than the other voles. This animal was in sparse grass growing among rocks on the dry, south slope of Heliograph Peak (2/5 mi. S). Oaks, locust, and *Ribes* grew along the slope. Other mammals caught were *Peromyscus boylii* and *Neotoma mexicana*. Trapping was continued for several days at this one spot, and it was not until the sixth day that the *Microtus longicaudus* was taken.

In some places, the voles were more active during daytime than at night. We could sometimes cause the voles to run across the traps and be caught merely by walking through the tall grass, making them scurry along their runways.

The type locality for *leucophaeus* has been given as "Graham Mountains," but it should be restricted to: near summit of Mt. Graham, about 10,000 feet, Graham Mts., Graham County, Arizona (see Allen, 1895:219). In collecting the type specimen on Mt. Graham, W. W. Price notes (in Allen, *loc. cit.*) that it was found along a boggy stream shaded with dwarf alders.

In August of 1951 and 1952, we collected thirty-two females that we judge to be sexually mature. Of these, ten were with embryos. Four females had four embryos, three had five embryos, and three had six embryos. At least three other females were lactating.

Average measurements, in millimeters, of twelve adult males and eight

adult females from Soldier Creek are: total length, 171.6, 184.9; tail, 52.8, 57.9; hind foot, 22.3, 21.9; ear from notch, 15.8, 15.8; greatest length of skull, 28.8, 29.3; occipitonasal length, 28.5, 29.0; basilar length, 24.8, 25.2; greatest zygomatic breadth, 16.1, 16.4; least interorbital constriction, 3.9, 3.9; length of nasals, 9.0, 9.1; alveolar length of upper molars, 7.0, 7.3. The race *leucophaeus* appears to be larger in many respects than *M. l. alticolus* and more yellowish than *Microtus longicaudus* subsp. from the White Mountains.

Specimens examined.—2/5 mi. S Heliograph Peak, 1; Snow Flat, 16; Treasure Park, 14; Hospital Flat Forest Camp, 8; Hospital Flat, 6; 1/3 mi. W Columbine Ranger Station, 7; Soldier Creek, 43; head Soldier Creek, 2; Goudy Canyon, 1; Chesley Flat, 2.

[*Ondatra zibethicus pallidus* (Mearns). Muskrat.—Two specimens of muskrat are recorded by Hollister (1911) from "Camp Grant." We assume that this was the Camp Grant on the San Pedro River, either at the mouth of Arivaipa Creek or where the San Pedro joined the Gila River, and not Fort Grant at the western base of the Grahams. We know of no muskrats anywhere in the Grahams at the present time.]

Erethizon dorsatum couesi Mearns. Porcupine.—Porcupines, in small numbers, inhabited the lower slopes, rarely the higher parts, of the Grahams. The porcupine collected near Cyclone Hill was found asleep under a yucca. In this locality, no trees were present, but prickly pear, cholla, and yucca predominated. This porcupine had been feeding on the fruit of the prickly pear; all of the intestinal tract was stained deep red from it. A specimen was killed on the road near Bonita in 1951. Droppings of porcupines were found in the crevices of large boulders at CN Ranch, 4900 ft., and along the road 2½ mi. S, 1 mi. E Maverick Mtn., 4600 ft. Both of these localities are in the oak belt. Reportedly a dog returned to the Angle Ranch with quills of a porcupine in its mouth. There is only one authentic report of the porcupine in the pine-fir belt. Steve Gallizioli saw one along the Swift Trail at Grant Creek, 8700 ft. Loggers, spending nearly all of their time in the pine-fir belt near the crest of the Mountains, had never seen a porcupine.

Our specimen is a young male with the last molar not yet erupted.

Specimen examined.—¼ mi. S Cyclone Hill, 1.

Lepus californicus eremicus Allen. Black-tailed jack rabbit.—Black-tailed jack rabbits were present but not numerous around the base of the Mountains. We saw rabbits as high as 5750 feet at Stockton Pass, but mostly below this elevation.

Specimen examined.—Stockton Pass picnic ground, 1.

Sylvilagus floridanus holzneri (Mearns). Eastern cottontail.—In our work in the Grahams, we saw only two rabbits high in the Mountains. We were able to collect one, which is immature. They were uncommon and exceedingly wary. On September 16, 1952, Steve Gallizioli saw three "mountain" cottontails at Columbine and was able to kill one. The animal was a female with four embryos, each about one and one-half inches long. The skin of this rabbit was sent us and we have prepared it, the best we could, into a study skin. We assume this specimen is *Sylvilagus floridanus holzneri* on an altitudinal basis and partly on color, but not on the basis of cranial features because the skull is completely crushed. It is impossible to determine the degree of fusion of the supraorbital process or the shape of the supra-

occipital shield. Hall and Kelson (1951) record *S. floridanus holzneri* from 6100 feet, along Ash Creek, in the Grahams. This locality is much lower than the 9500 feet where our *S. floridanus* were taken. The locality along Ash Creek is only about three miles above the Bird Farm, and Steve Gallizioli has seen no cottontails that he would regard as *S. floridanus* around or near the Farm in the several years he has been there.

Specimens examined.—Columbine Ranger Station, 2.

Sylvilagus audubonii cedrophilus Nelson. Desert cottontail.—Desert cottontails were present on the lower slopes and adjacent plains of the Mountains, and were numerous wherever ample cover was available. They were abundant at the Bird Farm, and some, less than half-grown, were seen there in mid-August. Cottontails were just as abundant in the thick sacaton near Bonita. Two females in late August were pregnant.

Neither Nelson (1909) nor Hall (1951a) record *Sylvilagus audubonii* from the Graham Mountains, but both indicate on their distribution maps that three different subspecies, *arizonae, minor, cedrophilus,* occur nearby. The nearest records are of *S.a. arizonae* from Willcox and Dos Cabezas. Four of our specimens are adults and in size average (in millimeters): total length, 404; tail, 50.5; hind foot, 99; ear, from notch, dry, 66. *S.a. cedrophilus* is the largest of the three subspecies in external measurements and specimens from the Grahams are even larger than Nelson's (1909) measurements of *cedrophilus*. One of our specimens is dark, much as in *S.a. cedrophilus;* the others show approach toward *S.a. arizonae* in color. We regard it advisable to refer the cottontails in the Grahams to *S.a. cedrophilus*. Furthermore, the Grahams are within 70 miles of the type locality of this subspecies.

Specimens examined.—1½ mi. S, 2 mi. W Maverick Mtn., 1; Marijilda Canyon, 4000 ft., 1; ¼ mi. E Marijilda Canyon campground, 1; ½ mi. NE C.C.C. camp, 1.

Pecari tajacu sonoriensis (Mearns). Collared peccary.—Peccaries or javelinas were present along the sides of the Grahams, with the possible exceptions of parts of the northeast side. They were most abundant, according to reports, on the southwest side. Mr. Dee Jernigan frequently saw bands of these "pigs" with young well up in the foothills. We saw the hide of a locally taken javelina at the 76 Ranch in the mouth of South Taylor Canyon. In March, 1953, Earl Long wrote me that javelinas were "on the increase at this time."

Odocoileus hemionus crooki (Mearns). Mule deer.—Mule deer were present in the foothills and on the flats adjacent to the Grahams, but not common at any place. Signs, probably of mule deer, were seen along the road east of Stockton Pass.

Mr. Dee Jernigan gave us the skull of an old buck from Mine Shaft Canyon, at the foot of Greasewood Mountain. This place is to the south of our study area, but the skull is worthy of special note. The longest rack of the antlers, along the central beam, measures 550 mm. from the bur to the tip. The tips of the antlers are bulbous, and appear somewhat palmate. We assume that Mr. Jernigan saved this skull because it was unusual.

Odocoileus virginianus couesi (Coues and Yarrow). White-tailed deer.—This small white-tailed deer, sometimes called Coues' whitetail, lived above

6000 feet in the Grahams. Along the Swift Trail, we encountered it from Wet Canyon to the top of the Mountains. In the flats or grassy meadows, white-tailed deer could be found almost every night. At Soldier Creek, a very reddish individual was present during the summer of 1951. On August 8, a fawn, not more than a few days old, was caught by hand at Snow Flat. The animal was judged to weigh between four and six pounds. It was bedded down in tall grass under a slanting, partially fallen, log. When released, the fawn awkwardly ran off to join its mother, who had returned to within 50 yards of us. On August 22, a spotted fawn was seen with a doe. During August, bucks were not often seen. One that we did see had velvet on the antlers.

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Natural Terrestrial Communities of Brewster County, Texas, with Special Reference to the Distribution of the Mammals[1]

H. Arliss Denyes
Florida State University, Tallahassee

The Big Bend region of Texas, with its abrupt changes in physiography and vegetation, offers excellent opportunity for field measures of the habitat restriction of mammalian species. Field studies were conducted in this region during a total of ten months in the spring of 1947 and the spring, summer and fall of 1948. The information secured concerning the distribution of the plants and mammals is presented here as a classification of the ecologic associations of Brewster County, Texas.

Although botanical and zoological information on the Big Bend of Texas has been published since 1880, there have been relatively few biologists who have visited this difficult area. The previous publications concerning both botanical and zoological investigations have been summarized by Anthony (1949), Blair (1950), Jameson and Flury (1949), and York (1949).

Methods for the Analysis of General Features

Associations

In order to obtain information about the natural communities of the Big Bend area transects, measured by car speedometer, were made along all the main highways and most of the passable back roads and trails. More detailed information about the plants in these associations was derived from series of 50-foot line transects taken during the analysis of the ecosystems for the restriction of certain of the small mammals. The scientific names of the plants follow Sperry (1938) and Sperry and Warnock (1941) and are listed in a sequence roughly approximating their relative abundance within each association rather than in any taxonomic order. In this study the term *association* is used to designate all the stands of a type of community which occur within a single life belt and a single biotic district.

The mammal records for these associations have been obtained by trapping, by observation and from information given by other authors. The identification of the larger mammals rests on the information given by Blair (1940) and Borell and Bryant (1942).

[1] The material for this publication was obtained during an expedition sponsored by the Botanical Gardens of the University of Michigan. The author was supported by fellowships from the Ontario Research Commission of Canada and Queen's University, Canada. The general classification of the ecologic associations of Brewster County, Texas and the measures of habitat restriction of certain of the small mammals were submitted as part of the requirements of the degree of Doctor of Philosophy at the University of Michigan under the supervision of Dr. Lee R. Dice whose help is gratefully acknowledged.

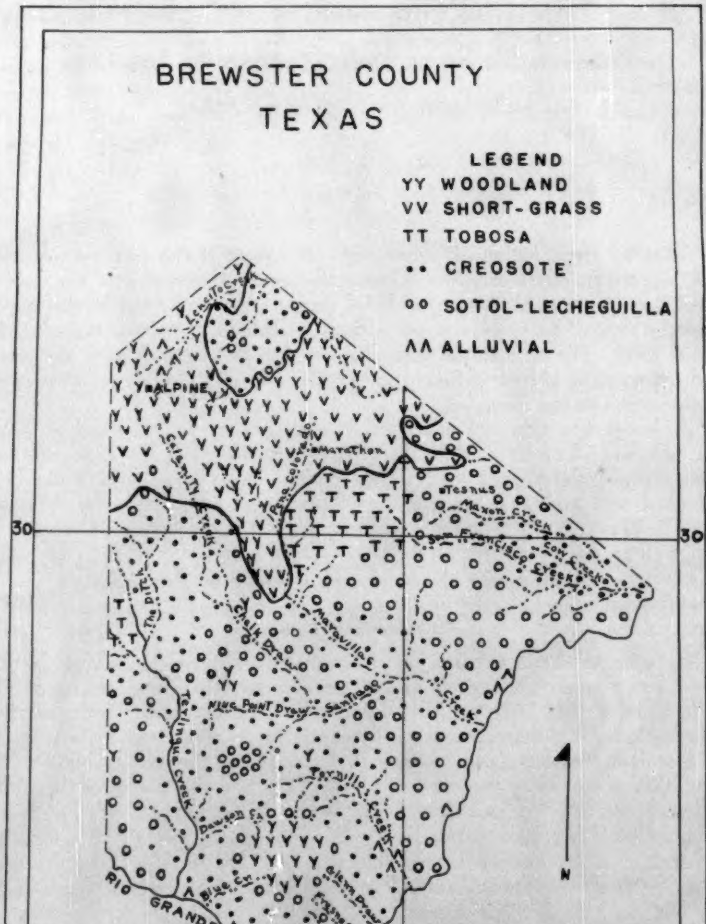

Fig. 1.—General vegetation types of Brewster County, Texas, showing the division of the Davis Mountain biotic district to the north and the Chisos biotic district to the south.

The distributional data obtained from these associations have been superimposed upon a regional base map oriented by the drainage pattern (fig. 1). A map of this kind is accurate only within two or three miles but is valuable as a pictorial representation of the distribution of the major associations of the region.

PHYSICAL FEATURES

Altitude was determined by altimeter and the United States Geological Survey Topographic maps. The exposure is expressed as compass direction and slope is given as degrees from the horizontal. Soil samples at six to ten inches depth in each stand were analyzed for texture by the sieve and hydrometric methods. The pH of each soil sample was taken with a Beckman potentiometer. The readings were taken from equal amounts of soil and distilled water allowed to stand for one half hour. No test of buffer capacity was made.

PRESERVATION OF SPECIMENS

Forty-three museum skins were made of representative specimens of small mammals. A further 544 specimens were preserved in 10% formalin. All specimens, accompanied by complete habitat notes, are deposited in the collection of the Museum of Zoology, University of Michigan.

General Physical Features of the Big Bend

The Big Bend region of Texas falls within the Basin Range Physiographic Province of Fenneman (1931). The main physiographic features are plateaus, mountainous ridges, volcanic necks, and basins or lowlands. Internal drainage is not uncommon in these basins and only a few streams have a constant flow of water throughout the year.

The main geologic uplifts in southwestern Texas occurred during the Appalachian and Laramide revolutions (Udden et al., 1916). The present highlands, remnants of once extensive plateaus, were formed, largely, during the Laramide revolution. Sedimentary beds, swamps, coal deposits and petrified trees were left by the epeiric seas which covered the land several times during the Paleozoic era and the Cretaceous period. During the Tertiary period and the Pleistocene epoch, igneous rock was intruded into these sedimentary deposits which, at present, are largely Lower Cretaceous Limestones.

The soils of the Big Bend of Texas have been studied as to their physical and chemical characteristics by Carter (1928) and also, to some extent, in relation to the vegetation by Carter and Cory (1932). Initially these soils can be divided into Highland and Lowland groups. The Highland soils are largely shallow and may have either a basic or acid reaction since they are derived from both limestone and igneous rocks. The Lowland group includes the alluvial and the basin soils which are deeper than the Highland soils and generally give a marked basic reaction.

According to Blair (1942), the Big Bend of Texas is in the subtropical belt of high pressure which produces xeric climates around the entire world. The winds come from the north and northwest in the winter, originating at a center of high pressure over the Great Basin. These winds lose their moisture as they move southward, and, instead of bringing rain, will often serve to rob

the area of what little moisture is present. In the summer, easterly winds blow toward a center of low pressure in Arizona but they also may have lost much of their moisture because of passing over areas of high surface temperatures. Being considerably southeast of the Arizona area of low pressure and closer to the Gulf of Mexico, the Big Bend of Texas usually receives heavy and fairly frequent rains during summer and early fall. The greater part of this precipitation is captured by the high slopes and surrounding plains of the Davis, Glass, and Chisos Mountains. During this time about two thirds of the annual rainfall occurs and the growing season closely approximates this period.

All the Big Bend region of the Texas is assigned to the Chihuahuan biotic province, Dice (1943). This includes the Stockton Plateau at the eastern edge of the area and the alternating desert plains and ranges to the west.

The Chihuahuan biotic province, in Brewster County, is divided into two biotic districts as defined by Dice (1943). The Davis Mountain biotic district includes the desert grassland and forested mountains of the northern part of the Big Bend region (Blair, 1940). The main mass of the Davis Mountains does not lie within Brewster County but the Del Norte and Glass Mountains, which are ranges of lesser magnitude, are found within the boundaries of northern Brewster County. Above 4,000 feet, these mountains support pines, oaks and junipers and are considered as part of the "Roughland life belt" of Blair (1940). The remainder of northern Brewster County is included in the "Plains life belt" of the Davis Mountain biotic district as defined by Blair (loc. cit.).

Much of the remainder of Brewster County is here assigned to a new biotic district to be called the Chisos biotic district, and which is distinguished, primarily, by large areas of creosote, tarbush, mesquite, ocotillo, prickly pears, sotol and lecheguilla. The associations of these various plants are somewhat further distinguished by their mammalian members. This Chisos biotic district has been previously included in the "Creosote Bush (Southern Desert Shrub)" region of the United States by Shantz and Zon (1924). The district was later described as belonging to the "Sotol-lecheguilla" and "Mountains" regions of Texas by Tharp (1928).

CHISOS BIOTIC DISTRICT

The Chisos biotic district extends north as far as the southern boundary of the Davis Mountain biotic district and also covers an area north of these mountains which is so far undetermined. The Chisos biotic district encompasses the true basin and range physiographic features of Brewster County. This basin and range physiography is of a less well defined type than that which occurs in the northern part of the Basin and Range province. Three ridges extend northwest-southeast into the Big Bend and lying between them are four lowland areas. The eastern ridge in the southern Big Bend area includes the block mountains of the Santiago and Dead Horse ranges. West of this a second ridge is formed by the Chinati and Bofecillos Mountains. The westernmost ridge includes only the Franklin Mountains near El Paso, Texas. The regular basin and range physiography is interrupted by the isolated masses of the Chisos, Rosillos, and Christmas Mountains in southern Brewster County. The basins separating the ridges are largely areas of sedimentation for the surrounding heights, although they were structural features originally.

A number of the larger rock masses of southern Brewster County consist

of dark, igneous rocks, mainly of a basaltic nature. Other ridges and plateaus have been formed from sedimentary rocks of varying ages and varying severity of tectonic upheaval. The masses of igneous rock, which comprise the greater part of the Chisos Mountains, arise with abruptness from the desert plains and attain a maximum altitude of 7,835 feet at Emory Peak. Although there are a number of deposits of Late Cretaceous limestones and clays throughout the Chisos Mountains, this huge rock citadel is primarily volcanic in origin. To the south, east, and west, isolated igneous mountains, such as Chilicotal, Talley, Lone, Castolon, and Kit, are scattered over the desert plains. To the north the low outlines of the Paint Gap and Grapevine Hills and the Rosillos Mountains interrupt the rolling floor of the Big Bend Basin and rise as igneous intrusions above its tertiary and quarternary gravels.

Farther to the west, Corazones Peaks stand like grim volcanic sentinels over the broken limestone mass of the Christmas Mountains. Deep within these mountains and in the Devils Graveyard of the Agua Fria quadrangle the red, yellow, white and blue of the Terlinqua beds are revealed by wind and water erosion.

Ten miles east of the Chisos Mountains, the block of uplifted sedimentaries of Boquillas limestone which form the Dead Horse Mountains, extend as several low ridges northwest to Dog Canyon and southeast into Coahuila, Mexico. In Brewster County the sheer side of this uplifted block faces east and in Coahuila an opposite torsion of the huge mass has presented a steep west wall. The Rio Grande has carved its Canyon of Boquillas at the point of torsion and then continues northeast along the Stockton Plateau. Two other sedimentary blocks, the Mesa de Anguila and Mariscal Mountain, have also given rise to deep canyons before the cutting power of the Rio Grande River.

Extending northwest from Dog Canyon, through which Nine-Point draw flows to join Maravillas creek, is the block of limestone known as the Santiago Mountains. This ridge is interrupted by the high saddle of Persimmon Gap and then continues northwest to eventually join the Del Norte Mountains. Along the western edge of the Santiago Mountains the igneous mass of Santiago Peak towers 3,000 feet above the nearby limestone ridge.

The soils of the Chisos biotic district, as found in southern Brewster County, include the Gila, Rio Grande, Reagan, Reeves, Ector and Brewster series. These soils can be classified on a physiographic basis. The Gila and Rio Grande series of soils occur in the flood plains and adjacent areas of the Rio Grande River and certain of its major tributaries. These soils are largely fine sandy and silt loams subject to flooding. They are friable, deep and have a basic reaction. Besides the cultivated crops which thrive on them, they support the baccharis and mesquite associations as well as a few scattered cottonwoods.

The soils of the basins belong largely to the Reeves gravelly and very gravelly loams. These soils are not rich in humus and give a basic or only slightly acid reaction. The Reeves series supports a predominant shrub growth including the creosote-tarbush, creosote-ocotillo-mesquite, creosote-tasajillo, and arroya associations. Occasional areas of Verhalen clay loams and silty clay loams support tobosa-shrub associations throughout the desert plains.

The gravelly-hill soil is a Reagan gravelly loam with a six to ten inch surface soil containing large quantities of smooth gravel often coated with

calcium carbonate. Below this there is a hard layer of caliche with embedded gravel. This gravelly-hill soil supports the sotol-sacahuiste association at the base of the Chisos Mountains.

The calcareous mountain and hill soils are the soils of the Ector series which are light brown, calcareous, friable and strong. In areas of sparse vegetation the soil may be almost white or yellow-white and is largely confined to the crevices of the rocky slopes. These soils were analyzed as fine sandy loam, silt loam and clay loam with a basic reaction. The Ector soils, in the Chisos biotic district, support the sotol-lecheguilla and creosote-lecheguilla associations. A few stands of pine occur on these soils in the Santiago and Chisos Mountains.

The soils of the Brewster series, found on igneous mountains and mesas, are brown or red, non-calcareous and friable. In many places the soil is found only in crevices and depressions. These soils, on analysis, are fine sandy loams, silt loams, clay loams, and loams. Although sparse these soils are sometimes rich in humus, often have a leaf litter and are usually acid in reaction. Forest communities of the higher life belts of the Chisos biotic district are found on these soils as well as sotol-lecheguilla and grama-bluestem associations at lower altitudes.

Climatic information for southern Brewster County is of a sporadic nature. The average yearly rainfall along the Rio Grande at Presidio is seven inches, but there may be as little as one or two inches a month during the rainy season. Rain may fall during any period of the year because of sporadic storms but rains sufficient to grow plants to maturity usually do not come until late summer and early fall. The abrupt topographic features result in further irregularities of rainfall, although the erratic movement of the storm areas seems to ensure a somewhat more even distribution of rainfall on opposing slopes than might be expected. Higher mountain masses, such as the Chisos, offer interesting rainfall patterns which are discussed by Muller (1937). From the few data available for the Chisos Mountains, the precipitation totals for the months of the years 1940, 1947, and 1948 range from 2 to 4 inches for May to August and as little as 0 to 1.61 inches from October to April. It seems reasonable to assume that it is the greater constancy of rainfall and the lesser degree of evaporation rather than the actual amount of rainfall which determines the relatively luxuriant vegetation of the Chisos Mountains.

Temperature data for southern Brewster County are rare. The average 1929 to 1948 is 68°F with an extreme range of 11 to 114°. The combination of high temperatures and low rainfall throughout much of the year undoubtedly determines, to the greatest extent, the domination of the desert shrubs over the grasses in most of the Chisos biotic district.

In the Chisos biotic district, the basin associations are dominated by desert shrubs, such as creosote, tarbush, acacias, blackbush, yucca, and ocotillo. Low hills, mountains and mesas are covered with sotol, lecheguilla, and their various associates. The higher mountains and mesas support communities of the woodland climax as well as more xeric types below the wooded areas. In the valley of the Rio Grande, there is an alternation between areas of deep, alluvial soil, with their rich communities, and the steep canyons of the block mountains at Santa Elena, Mariscal, and Bouquillas with rocky, talus slopes and little stable soil.

DESERT PLAINS LIFE BELT

The true desert plains of Brewster County are areas of sedimentation from the surrounding hills and mountains. The drainage is intermittent and several channels eventually lead to the Rio Grande River. A number of low, igneous outcrops interrupt the rolling basins and in certain areas there are well dissected badlands. The desert plains extend from approximately 2,000 to 3,500 feet elevation. The rainfall is sporadic and apparently averages less than ten inches a year, although weather stations have been fully operating only within very recent times. The range of temperature for the desert plains is between 10 and 120°F, as far as can be determined.

The valley of the Rio Grande, in Brewster County, only occasionally widens to form alluvial deposits which support a rich growth of several associations. In the narrow canyons of Mariscal, Santa Elena, and Boquillas, there is little room for the growth of distinct plant associations.

Riverbank association

Procyon lotor mexicanus, Raccoon	Signs
Castor canadensis mexicanus, Beaver	Signs

The riverbank association is not characterized by any definite group of plants. Occasionally mesquite, baccharis, willow, or cottonwood overhang the water, but usually there are exposed flats of silt and coarse gravel between the vegetation and the river. No plants grow on these flats, since they are subject to frequent flooding.

The only mammal known to live in the river banks and, therefore, which truly characterizes this association is the beaver. These are bank beaver, and the only evidence of their presence is found in the cut vegetation along the river. A specimen reported by Borell and Bryant (1942) is assigned to *mexicanus*. Tracks of the raccoon were seen on the river flats at Santa Elena and Reagan canyons. Tracks of large mammals, which more commonly frequent other associations in the area, were seen along the river flats. These include skunk, mountain lion, bobcat and mule deer.

Baccharis association

River bottom association (in part) Borell and Bryant (1942).

Conepatus mesoleucus mearnsi, Hog-nosed skunk	Sight
Cratogeomys castanops lacrimalis, Plateau pocket gopher	1
Perognathus merriami gilvus, Merriam pocket mouse	3
Perognathus penicillatus eremicus, Desert pocket mouse	24
Sylvilagus audubonii, Audubon cottontail	Sight

On the fine sandy loams of the Rio Grande valley and in the broad arroya bottoms of the nearby desert plains, where the water table is high, *Baccharis glutinosa* grows in fairly dense and homogeneous stands. The soil is deep, moist below the first three inches, and gives a pH of approximately nine. Occasionally white patches of accumulated salts are present in bare areas.

According to Sperry (1938), *Baccharis neglecta* and *B. salicina* are also found in this association and are more abundant than *B. glutinosa* in certain places. Where the growth is more open, as at Santa Elena canyon, *Bouteloua barbata* may occur sparsely as well as colonies of *Nerisyrenia camporum* and

Aplopappus spinulosus. The most effective ground and crown cover, however, is supplied by the various species of *Baccharis*.

Small mammal burrows are common in the baccharis association, especially in the mounded soil at the base of shrubs. The most common small mammal is the desert pocket mouse. The tiny Merriam pocket mouse is not abundant here but occurs fairly commonly in the adjoining association of creosote and ocotillo. There were fresh gopher mounds about every twenty feet throughout one *Baccharis* stand near Castolon. No specimen of the Ord kangaroo rat (*Dipodomys ordii attenuatus*) was obtained, but it is reported from a river bottom association at Johnson's ranch and at the mouth of Santa Elena canyon by Borell and Bryant (1942). The deer mouse (*Peromyscus maniculatus blandus*) and the hispid cotton rat (*Sigmodon hispidus berlandieri*) are also listed by these authors as occurring almost entirely in this association.

The larger mammals are not confined to the baccharis association, but certain of them were regularly observed while the area was being studied. Among the most common was the hog-nosed skunk, which was seen almost every evening, and the Audubon cottontail.

Mesquite association

Mesquite association Shantz and Zon (1924); *River bottom association* (in part) Borell and Bryant (1942).

Bassariscus astutus flavus, Ringtail cat	Signs
Conepatus mesoleucus mearnsi, Hog-nosed skunk	Sight
Taxidea taxus berlandieri, Badger	Signs
Canis latrans texensis, Coyote	Sight
Perognathus penicillatus eremicus, Desert pocket mouse	20
Dipodomys merriami ambiguus, Merriam Kangaroo rat	9
Peromyscus eremicus eremicus, Cactus mouse	5
Neotoma micropus canescens, Baird woodrat	Signs

The mesquite association may consist of a thin line of plants, predominantly *Prosopis glandulosa*, or of an extensive area of thick growth adjacent to the creosote flats along the Rio Grande and its larger tributaries, such as Terlingua and Tornillo creeks. The association is found on gently sloping areas with fine sandy loams, above the level of the baccharis. The soil gave a pH from 7.9 to 8.4 from three different locations. The sandy loam is easily broken, although the surface will bake hard in open places after flooding.

When this association is extensive it consists of a number of plant genera, several presenting much the same appearance. The common shrubs are *Prosopis glandulosa, Strombocarpa odorata, Condalia spathulata* and *Tamarix gallica*. The ground cover sometimes consists of a sparse growth of *Sporobolus cryptandrus, Aristida glauca*, and *Triodia pulchella*, but the soil is often bare. In more open areas of the thicket, as at Castolon, a thin growth of *Atriplex canescens* and *Cassia bauhinoides* is found. Cacti, such as *Opuntia phaeacantha, O. leptocaulis*, and *Echinocereus dasyacantha* may also be present, especially at the base of shrubs.

Small mammals of several species are abundant in the mesquite association. The desert pocket mouse is the most common small mammal of the association. The Merriam kangaroo rat is apparently a staple member, but does not reach its greatest abundance here. The cactus mouse was taken in each trap-

ping location although it appears to be more abundant in other associations of the area.

A few houses of the woodrat were present in the thickets. Diggings of the hog-nosed skunk were seen in several places as well as several large excavations made by a badger. A pack of three coyotes was once observed in the mesquite association at Castolon, but the coyote is more common on the desert flats and mesas.

Creosote-Tarbush association

Black bush (Flourensia cernua) association Shantz and Zon (1924); *Larrea-flourensia associes* Weaver and Clements (1929); *Larrea-flourensia desert scrub* Muller (1940); *Desert flat association* (in part) Borell and Bryant (1942).

Dipodomys merriami ambiguus, Merriam Kangaroo rat	14
Perognathus merriami gilvus, Merriam pocket mouse	6
Perognathus penicillatus eremicus, Desert pocket mouse	2
Perognathus nelsoni canescens, Nelson pocket mouse	3
Peromyscus eremicus eremicus, Cactus mouse	4
Neotoma micropus canescens, Baird woodrat	1
Lepus californicus texianus, Black-tailed jackrabbit	Sight
Sylvilagus audubonii, Audubon cottontail	Sight
Pecari angulatus angulatus, Javelina	Sight
Odocoileus hemionus crooki, Mule deer	Sight

Creosote (*Larrea divaricata*) and tarbush (*Flourensia cernua*) together dominate large areas of the Desert Plains life belt in Brewster County. This association is rare in Presidio County. Most of the cover is at crown height and much bare ground is exposed. The soils are deep and include the silt and clay loams with a range of 8.1 to 8.6 in pH. Although the silt and clay content is high, the persistently dry conditions have resulted in a powdered rather than a packed type of soil.

If the Chisos biotic district of the Chihuahuan biotic province is climatically determined rather than the result of land misuse, the creosote-tarbush association can be considered as the climax vegetation for the desert plains in this region. Because of heavy overgrazing in Brewster County it is difficult to draw any definite conclusions regarding the climax. In his climatic and ecologic treatment of Chihuahua, Mexico, LeSuer (1945) stated that he believed the desert shrub to be climatically determined in eastern Chihuahua, although it is undoubtedly occupying former grassland in many areas. Muller (1940), in a study of the Big Bend Region of Texas, claims that many facts point to "Larrea-Flourensia" as having the ability of autosuccession and definitely forming a stable climax. The elimination of grazing within the Big Bend National Park should eventually lead to the correct determination of the natural climax of the area.

Where the communities of the Chisos biotic district have invaded the grasslands around the Davis Mountains the determining factors appear to be edaphic. The creosote-tarbush association occurs in these northern parts, as in the south, on silt and clay loams in fairly level areas. In the north the tarbush also grows in pure colonies, having invaded former tobosa land.

Some shrub associates of the creosote and tarbush, in the southern part of Brewster County, are *Parthenium incanum, Krameria gravi, Leucophyllum minus, Ephedra trifurca, Jatropha spathulata, Fouquieria splendens, Prosopis*

glandulosa, Koeberlinia spinosa, Acacia constricta, A. greggii, Mimosa biuncifera, Chilopsis linearis, Microrhamnus ericoides, Yucca torreyi, and *Y. baccata.* The ground cover is largely supplied by clumps of *Agave lecheguilla,* by the cacti, *Opuntia engelmannii, O. leptocaulis, Echinocereus stramineus,* and *E. enneacanthus,* and by the grasses, *Aristida glauca,* and *Triodia pulchella.* In Dagger flats the huge *Yucca carnerosa* appears to dominate what actually are creosote-tarbush and sotol-lecheguilla associations.

In the north, areas of creosote and tarbush also support *Prosopis glandulosa, Acacia constricta, Microrhamnus ericoides, Koeberlinia spinosa, Rhus trilobata, Berberis trifoliata, Yucca torreyi, Y. elata,* and *Nolina texana.* Colonies of *Gutierrezia* often occur in low places. The cacti are *Opuntia engelmannii, O. leptocaulis,* and *Echinocereus enneacanthus.* The common grasses are *Hilaria mutica, Seleropogon brevifolius, Sporobolus cryptandrus, Aristida purpurea,* and *Bouteloua gracilis.*

The most common small mammal of the creosote-tarbush association is the Merriam kangaroo rat. No specimen of this rat was ever taken from the sotol-lecheguilla association which is frequently within 50 feet of the creosote and tarbush. The three species of pocket mice native to the area are usually found in this association, but the Nelson pocket mouse is more abundant in rocky habitats. The cactus mouse is present in most habitats which have a soft soil. The mule deer range through several associations, and were frequently observed in the creosote-tarbush association. A small herd of 8 javelina were once observed in this association after nightfall.

Creosote-Ocotillo-Mesquite association

Fouquiera subclimax Weaver and Clements (1929); *Desert flat association* (in part) Borell and Bryant (1942).

Taxidea taxus berlandieri, Badger	Sight
Lynx rufus baileyi, Bobcat	Signs
Citellus interpres, Texas antelope squirrel	Sight
Citellus spilosoma major, Spotted ground squirrel	Sight
Thomomys bottae limitaris, Botta pocket gopher	Signs
Dipodomys merriami ambiguus, Merriam kangaroo rat	6
Perognathus merriami gilvus, Merriam pocket mouse	20
Perognathus penicillatus eremicus, Desert pocket mouse	4
Perognathus nelsoni canescens, Nelson pocket mouse	12
Peromyscus eremicus eremicus, Cactus mouse	18
Lepus californicus texianus, Black-tailed jackrabbit	Sight
Odocoileus hemionus crooki, Mule deer	Sight

In the somewhat higher areas with gravelly and stony loams, creosote grows with ocotillo and mesquite in a barren community. The soil belongs to the Reeves series and contains many pebbles, which, at the surface, are arranged in the typical desert pavement. A frequent plant is *Prosopis glandulosa,* which takes on a treelike growth. There are also occasional clumps of lecheguilla in the more stony parts of the association. There is little effective cover, either at the ground or crown levels. This growth of creosote, ocotillo, and mesquite is very common between the Rio Grande and the foothills of the Chinati Mountains in Presidio County, on the flats north of the Chisos Mountains, and along the roads to Hot Springs and Santa Elena canyon in Brewster County.

Other associated shrubs and herbs are *Yucca torreyi, Acacia greggii, A. berlandieri, Jatropha spathulata, Ephedra antisyphilitica, Porlieria angustifolia,*

Leucophyllum minus, Agave lecheguilla, and *Croton neomexicana.* The cacti are *Opuntia engelmannii, O. grahami, O. rufida, O. leptocaulis, O. macrocentra, Echinocereus enneacanthus,* and *E. stramineus.* Grasses are very sparse and include *Bouteloua breviseta* and *Triodia pulchella.*

The Merriam pocket mouse is abundant in this association, although the ground is fairly hard. The Nelson pocket mouse occurs only where the creosote-ocotillo-mesquite association slopes abruptly toward the river-bottom associations. These slopes are more uneven than the flats and only slightly more rocky. The cactus mouse is abundant on the fairly close packed soil of the level parts of the association. The antelope squirrel and the spotted ground squirrel are not abundant in this association, but are usually seen wherever there are outcrops of rock. Carcasses of bobcat were frequently seen hanging from fences in this association.

Creosote-Tasajillo association

Desert flat association (in part) Borell and Bryant (1942).

Citellus spilosoma major, Spotted ground squirrel	1
Dipodomys merriami ambiguus, Merriam kangaroo rat	9
Perognathus merriami gilvus, Merriam pocket mouse	2
Perognathus penicillatus eremicus, Desert pocket mouse	15
Peromyscus eremicus eremicus, Cactus mouse	7

In some of the lower, washed areas of the desert plains, creosote grows with plants other than ocotillo in a less barren community. *Yucca torreyi,* and *Y. baccata* are usually the tallest plants present, while tasajillo (*Opuntia leptocaulis*) is common and often twined about the lower branches of the creosote bushes. Scattered mesquites are also typical of this association as well as large clumps of platyopuntias. The soil is coarse sandy to clay loam with a pH of 8.4 to 9.0.

The creosote-tasajillo association is favored by the desert pocket mouse, possibly because of the loose soil. The Merriam pocket mouse is scarce in this association, which is subject to washing. In Tornillo Flat many kangaroo rat mounds about six feet in diameter and sometimes three feet high were observed. In one mound there were thirty burrow openings to a square yard. One female ground squirrel, with three embryos, was caught in a creosote-tasajillo association on May 1, 1947.

Tobosa-Burrograss association

Hilaria climax (Lake bed clay) Campbell (1931); *Hilaria mutica postclimax* Cottle (1931); *Hilaria mutica preclimax facies* LeSuer (1945); *Tobosa-grama association* York (1949).

Citellus mexicanus parvidens, Mexican ground squirrel	3
Perognathus merriami gilvus, Merriam pocket mouse	1

Scleropogon brevifolius appears first on clay soils following dry conditions and is soon followed by *Hilaria mutica* (Campbell, 1931). The burrograss occurs largely on areas slightly higher than the *Hilaria* dominated flats. During early succession, there is slight mixing of the two grasses, and they then occur in colonies of varying frequency depending on the stage.

Pure stands of *Hilaria* and *Scleropogon* without accompanying shrubs are not common in the Big Bend region today. One large tobosa flat, west of the Glass Mountains, was studied. The soil is clay with a pH of 8.8. The asso-

ciated plant species include *Sporobolus cryptandrus, Bouteloua gracilis, B. hirsuta, B. curtipendula, Aristida pansa, Panicum obtusum, Muhlenbergia repens, M. arenacea, M. arenicola,* and *Gutierrezia* sp.

Mammals, except for the Mexican ground squirrel, are scarce in the tobosa-burrograss association. Although there is a good ground cover, there is little variety of food and the soil is very hard.

Tobosa-Mesquite association

Mesquite-grass associes Shantz and Zon (1924); *Short-grass-mesquite association* Blair (1940); *Desert flat association* (in part) Borell and Bryant (1942).

Mephitis mephitis varians, Plains skunk	Sight
Conepatus mesoleucus mearnsi, Hog-nosed skunk	Sight
Citellus spilosoma major	Sight
Citellus mexicanus parvidens, Mexican ground squirrel	Sight
Dipodomys merriami ambiguus, Merriam kangaroo rat	1
Perognathus merriami gilvus, Merriam pocket mouse	2
Reithrodontomys megalotis megalotis, Desert harvest mouse	1
Peromyscus leucopus tornillo, Wood mouse	1
Peromyscus boylii attwateri, Brush mouse	3

The occurrence of many areas in the Big Bend of Texas where the mesquite is a very obvious and evenly distributed member of the tobosa flats makes the recognition of this association reasonable. South of the transition between the Davis Mountin and Chisos biotic districts the mesquite of the tobosa flats has a tree-like form, while the mesquite found in the flats nearer the grasslands has a low bush form, often levelled off about two feet from the ground. It is not known whether these are different species or the result of an environmental effect. The spindly mesquite bushes of the south grow closer together in thickets, while the low bushes of the north are scattered over the flats about twenty or thirty feet apart. In the south the grass associates are largely *Scleropogon brevifolius, Sporoblus cryptandrus,* and *Muhlenbergia repens. Larrea divaricata, Acacia constricta, Opuntia imbricata, O. leptocaulis,* and *O. macrocentra* are sometimes scattered sparsely through the association.

Isolated tobosa-mesquite associations were studied or observed in several places in the desert plains. One, east of the Santiago Mountains about latitude 20, was briefly studied. Another was observed just west of Mariscal Mountain, a third about three miles west of Nine-Point Mesa and another near the 02 ranch was trapped. Green Valley has a rich association of tobosa and mesquite, while several badly eroded areas occur ten miles east of Alpine, Texas. All of these stands have a gentle slope and were common to silty clay loams with a pH of 8.4 to 9.3. The water retention, followed by desiccation, packs the constituents of these soils.

The characteristics of this association are a mixture of grassland and brushland. The mammalian members are, therefore, derived from both grass and brush inhabiting species. None of these mammals is abundant in the tobosa-mesquite association, except the ground squirrels. The varied potentialities in both food and cover in this association, as compared to the tobosa-burrograss association, has resulted in a greater wealth of species.

Tobosa-Platyopuntia association

Citellus mexicanus parvidens, Mexican ground squirrel	Sight
Perognathus merriami gilvus, Merriam pocket mouse	5

The presence of regularly distributed clumps of platyopuntias in otherwise pure stands of tobosa grassland is common in Brewster County. Whether this is natural or the result of land misuse, a characteristic community has resulted and deserves recognition. The largest areas of this association were observed on the road from Alpine to Terlingua, south of Whirlwind and Mitchell Mesas. Another extensive community was studied on the Gage Estate east of Marathon. The soil is clay loam (pH 8.6). The tobosa grass grows in tussocks with narrow ribbons of bare soil between the grass clumps. According to Anthony (1949), the common species of cacti are *Opuntia tortispina* and *O. setispina* in the Davis Mountain area and *O. macrocentra* in the southern part of Brewster County.

The most common mammal in the tobosa-platyopuntia association, as in the tobosa-burrograss association, is the ground squirrel. Where the hard ground is broken by the diggings of the ground squirrel, small burrow holes, possibly belonging to the pocket mouse, can be seen. It is likely, however, that the greater number of pocket mice in this association than in the tobosa-burrograss is a result of the abundant opuntia seeds. Pockets of three of these five small mice were packed entirely with opuntia seeds.

Tobosa-Tarbush association

Flourensia-hilaria climax (Gravelly clay loam) Campbell (1931); *Flourensia cernua society,* Cottle (1931).

Perognathus merriami gilvus, Merriam pocket mouse	14
Peromyscus maniculatus blandus, Deer mouse	2
Peromyscus leucopus tornillo, Wood mouse	2
Lepus californicus texianus, Black-tailed jackrabbit	Sight

In northern Brewster County the tarbush (*Flourensia cernua*) has invaded tobosa flats in several places. The soil of these invaded tobosa flats is a silty clay loam (pH 8.7), and subject to slight washing. These areas have a greater degree of slope than the other tobosa associations and the grass cover is sparse with considerable exposed ground, especially around the bushes. Some of the other plants in this association are *Acacia* sp., *Mimosa dasyacarpa, Leucophyllum* sp., *Euphorbia* sp., *Dalea frutescens, Gutierrezia* sp., *Croton neomexicanus, Zinnia* sp., and *Aristida glauca.* The whole association is arid and open with the shrubs usually spaced two or three feet apart.

This association is dissimilar to the other tobosa communities in having more loose soil and much less ground cover. As a result, *Perognathus merriami gilvus* is abundant in the tobosa-tarbush association. The deer mouse and wood mouse are more abundant in other associations, although neither of these mammals was caught very frequently during this study.

FOOTHILLS LIFE BELT

The Foothills life belt associations are found on the mountain ranges and low hills from 3,500 to 4,500 feet elevation within the Chisos biotic district. The climatic conditions are somewhat different than those of the Desert Plains life belt because of the factors of altitude and exposure. Many of the ranges are not high enough to capture considerable rainfall, like the Chisos Mountains, but probably receive more rainfall than the desert plains. Actual climatic data for the desert range in Brewster County are negligible. At Persimmon Gap, in the Dead Horse Mountains, the total precipitation for 1946 was 4.78 inches,

for 1947, 4.15 inches, and for 1948, 3.88 inches. The conditions for grass on the ranges are superior to those on the desert plains and these low, desert ranges support a relatively luxuriant growth of short grasses in most places.

Chert-Hill association

Perognathus merriami gilvus, Merriam pocket mouse 6

Tangled growths of acacia are typical of the low, chert hills of the Southern Marathon region. The common acacia, mostly *A. vernicosa,* is accompanied by *Microrhamnus ericoides, Yucca torreyi, Leucophyllum* sp., and *Opuntia* sp. The sparse ground cover, other than the cacti, consists of species of *Bouteloua* and *Aristida.* The soil is crumbly and coarse, forming a fine sandy loam in the crevices. The pH obtained was 7.7 and the texture is coarse since the surface consists largely of rubble with solid rock underneath.

The only mammal caught in this association was the Merriam pocket mouse. A grasshopper mouse and a harvest mouse were taken in the adjacent short-grass-yucca association as well as seven of the same species of pocket mouse.

Sotol-Lecheguilla association

Lecheguilla-sotol associes Shantz and Zon (1924); *Sotol-lecheguilla region* Tharp (1928); *Sotol postclimax* Weaver and Clements (1929); *Lower foothill association* (in part) Borell and Bryant (1942).

Citellus variegatus couchii, Rock squirrel .... Sight
Perognathus merriami gilvus, Merriam pocket mouse 1
Perognathus penicillatus eremicus, Desert pocket mouse 1
Perognathus nelsoni canescens, Nelson pocket mouse 8
Peromyscus eremicus eremicus, Cactus mouse 14
Odocoileus hemionus crooki, Mule deer .... Sight
Odocoileus virginianus carminis, White-tailed deer .... Sight

An association, dominated by *Dasylerion leiophyllum* and *Agave lecheguilla,* occurs on the steep slopes of almost all the low mountains and mesas of both limestone and igneous rock. The scant soils include the fine sandy, silt, and silty clay loams. The pH of the igneous and limestone soils is similar, giving a range of 8.2 to 8.6 for igneous areas and 8.0 to 8.9 for limestone areas. There is a great exposure of solid rock.

The Dead Horse, Santiago, and Mariscal Mountains, as far north as latitude 25 degrees, as well as many outlying igneous masses such as Talley, Chilicotal, and Lone Mountains, present a solid growth of sotol, lecheguilla, and their associates. *Agave lecheguilla* forms dense colonies in this association and is the most abundant member, although *Dasylerion leiophyllum* has the appearance of greater dominance because of its life form. Many height classes are represented in the plants of this association. The grass cover is fairly rich on staple slopes, especially about the base of prickly plants and among the lecheguilla.

The common plants associated with the sotol and lecheguilla are *Fouquieria splendens, Jatropha spathulata, Euphorbia antisyphilitica, Hechtia scariosa, Dalea wrightii, Yucca torreyi, Larrea divaricata, Parthenium incanum, P. lyratum, P. argentatum, Ephedra trifurca, Rhus microphylla, Acacia* sp., *Opuntia rufida, O. grahami, O. phaeacantha, Croton neomexicana, Selaginella rupestris, Bouteloua gracilis, B. hirsuta, B. curtipendula, B. breviseta, Aristida glauca, Eragrostis intermedia, Hilaria berlangeri,* and *Triodia pilosa.* The greatest

amount of ground cover is supplied by the colonies of lecheguilla, the grass clumps, and occasional thick growths of *Euphorbia antisyphilitica* (candelilla) and *Hechtia scariosa.*

The sotol-lecheguilla association is not productive of a variety of small mammals. The population is largely represented by the cactus mouse and the Nelson pocket mouse. In both the desert and the grassland of Brewster County, habitats dominated by sotol and lecheguilla are favored by the cactus mouse. The Nelson pocket mouse is seldom found in associations on the desert that do not have considerable slope. The white-tailed deer is only rarely seen in the sotol-lecheguilla associations, but the mule deer is common.

Creosote-Lecheguilla association

Perognathus penicillatus eremicus, Desert pocket mouse	1
Perognathus nelsoni canescens, Nelson pocket mouse	1
Peromyscus maniculatus blandus, Deer mouse	1
Peromyscus eremicus eremicus, Cactus mouse	5
Neotoma micropus canescens, Baird woodrat	1

Just below the sotol-lecheguilla association, on the desert ranges, there will often be an area dominated by creosote and lecheguilla. This may occur rather extensively, as along the base of the Dead Horse Mountains. In other places, as near Solis ranch, low, limestone cuestas exhibit this community as the entire cover. The lecheguilla is sparsely distributed and the creosote bushes are scattered in a fairly regular pattern along the terraced slopes. Much bare rock is exposed, with the pockets of soil supporting shrubs like *Krameria grayi, Fouquieria splendens, Ephedra* sp., and *Leucophyllum frutescens. Opuntia grahami* and *Echinocereus dasyacantha* are the common cacti. The few, scattered clumps of the grasses, *Bouteloua gracilis, B. breviseta, Aristida* sp., and *Triodia pulchella,* offer little ground cover. The soil in the crevices is clay to sandy clay loam (pH 9.1).

The creosote-lecheguilla association is one of the most barren communities in the desert. Crevices of soil for digging burrows are few and plants such as creosote, cacti, and grass, whose seeds were most represented in the mouse pockets, are sparse. The most typical mammalian member of the association is the cactus mouse.

Sotol-Sacahuiste association

Lower foothill association Borell and Bryant (1942).

Taxidea taxus berlandieri, Badger	Sight
Urocyon cinereoargenteus scottii, Gray fox	Sight
Canis latrans texensis, Coyote	Sight
Thomomys bottae limitaris, Botta pocket gopher	Signs
Perognathus nelsoni canescens, Nelson pocket mouse	Reported*
Reithrodontomys fulvescens canus, Fulvous harvest mouse	Reported*
Sigmodon ochragnathus, Mountain cotton rat	Reported*
Sylvilagus robustus, Mountain cottontail	Reported*
Pecari angulatus angulatus, Javeline	Sight
Odocoileus hemionus crooki, Mule deer	Sight

The foothills of the Chisos Mountains lie close to the main mass and extend from 3,500 to 4,500 feet elevation. There is a somewhat more pronounced outlying foothills situation along part of the southern edge of these

* Borell and Bryant, 1942.

mountains, but generally the foothills blend into the precipitous slopes of the mountains. The climatic conditions, at this altitude, tend toward aridity and an association, which is somewhat intermediate between the truly arid conditions of the desert plains and the mesophytic nature of the higher mountains, has developed.

The foothills of the Chisos Mountains support a community which on first sight bears considerable similarity to a rich sotol-lecheguilla association of a desert range. The sacahuiste (*Nolina texana*), however, is a dominant member of this association and the lecheguilla grows more sparsely. The grass associates are most luxuriant on the east and southfacing slopes, which catch the prevailing winds. The sotol-sacahuiste association on the south slope of the Chisos Mountains leading up to Pine Canyon presents an exceptionally rich growth of grasses, including such species as *Andropogon barbinodis, Heteropogon contortus, Muhlenbergia pauciflora, Boutelous curtipendula, B. hirsuta, Aristida adscensionis, Triodia pulchella, T. pilosa,* and *T. grandiflora.* The common shrubby plants of this association are *Prosopis glandulosa, Koeberlinia spinosa, Berberis trifoliata, Acacia* sp., *Yucca torreyi, Microrhamnus ericoides,* and *Opuntia engelmannii.* The soil is a gravelly loam and a layer of considerable depth has accumulated on top of the solid rock.

No trap lines were set in the sotol-sacahuiste association. Sight records and information given by Borell and Bryant (1942) indicate that this is a productive association for mammals. Species are represented from the desert and from the higher parts of the Chisos, which is in keeping with the intermediate conditions of climate and cover. The mule deer is very abundant here. This association probably represents the most extreme conditions of aridity tolerated by the fulvous harvest mouse in this desert region.

ENCINAL LIFE BELT

The encinal life belt includes the steep slopes, basins and canyons of the upper Chisos. This belt extends from 4,500 to 7,835 feet elevation and is characterized by tree growth, although several grassy areas occur on the lower slopes and in the basins.

The Chisos Mountains arise abruptly from the desert plains to an elevation of 7,835 feet at Emory Peak. As a result, a mesophytic oasis, luxuriant in comparison to the surrounding plains, has developed. The mass of the Chisos is igneous, the slopes are precipitous and two basins occur at different elevations. The lower basin, at 5,000 feet, is deep and ringed by steep slopes with narrow canyons. The higher basin, known as "Laguna" is shallow and occurs at 1,000 feet or more above and to the south of the main basin. A distinct association of grasses has developed in this upper basin.

The southern edge of the Chisos is broken by deep canyons rimmed by hogbacks that reach out onto the desert plains. From the South rim of the Chisos Mountains the whole bend of the Rio Grande is spread out in panoramic glory. Within the deep canyons the greater retention of moisture has given rise to remnants of the Rocky Mountain transition zone, not found elsewhere in the Big Bend region.

During the summer, there are daily afternoon rains resulting from the differential heating of the mountains and the desert plains (Muller, 1937). Throughout the year any moisture laden wind striking the steep sides of the

Chisos will rise, expand, cool and bring rain to the mountains. Unless general conditions become very dry, as during the years of 1947 and 1948, several springs run in the upper Chisos, but the canyons do not have a very heavy flow of water except after a rain. The temperature, in summer, seldom rises above 90°F in the higher Chisos, while light snow and freezing temperatures are usual each winter.

Oak chaparral association

Chaparral division Shantz and Zon (1924); *Petran chaparral* subclimax Weaver and Clements (1929).

Citellus interpres, Texas antelope squirrel	Sight
Peromyscus pectoralis laceianus, Encinal mouse	2
Sigmodon ochragnathus, Mountain cotton rat	2
Lepus californicus texianus Black-tailed jackrabbit	Sight
Sylvilagus audubonii, Audobon cottontail	Sight

A narrow, interrupted belt of scrub oak occurs in the Chisos Mountains at an elevation of about 4,000 feet. The oaks (*Quercus grisea* and *Q. gravesii*) have a low, shrubby life form and are accompanied by *Juniperus monosperma* and mountain mahogany (*Cercocarpus eximius*). The ground cover consists of clumps of *Agave lecheguilla, Bouteloua gracilis,* and *Muhlenbergia emersleyi.* The ground is rocky and the soil a sandy loam with a 7.5 pH. There is more brushy shelter here than in many of the other associations of the mountains. This chaparral association lies between the grama-bluestem or sotol-sacahuiste associations and the pinyon-oak-juniper association of the higher altitudes.

The brushy nature of this association provides good cover for the jackrabbit and the cottontail. The jackrabbit was not seen in the other associations at higher altitudes. The encinal mouse is typical of marginal areas where woodland merges into grassland type. This transition between woodlands and grasslands is also the favored habitat of the mountain cotton rat.

Pinyon-Oak-Juniper association

Pinyon-juniper Shantz and Zon; (1924) *Pinus-juniperus* Weaver and Clements (1929).

Ursus americanus amblyceps, Black bear	Reported
Bassariscus astutus flavus, Ringtail cat	Sight
Mephitis mephitis varians, Striped skunk	Reported*
Conepatus mesoleucus mearnsi, Hog-nosed skunk	Sight
Felis concolor stanleyana, Cougar	Reported
Lynx rufus baileyi, Bobcat	Reported
Citellus variegatus couchii, Rock squirrel	Sight
Citellus interpres, Texas antelope squirrel	Sight
Peromyscus boylii rowleyi, Brush mouse	1
Peromyscus pectoralis laceianus, Encinal mouse	4
Peromyscus eremicus eremicus, Cactus mouse	2
Neotoma albigula albigula, White-throated woodrat	Reported*
Sylvilagus robustus, Mountain cottontail	Sight
Odocoileus virginianus carminis, White-tailed deer	Sight

The high slopes of the Chisos Mountains (5,000 to 8,000 feet) support a rich vegetation compared to that of the desert plains. Pines, many oaks, and junipers are the dominating species. The Chisos Mountains shelter many

* Borell and Bryant, 1942.

species of oaks, some of which occur commonly in the mountain systems to the north, others of which have their greatest abundance in the Sierra del Carmen of Mexico (Muller, 1937). The common oaks of the dry slopes are *Quercus emoryi, Q. gravesii,* and *Q. grisea,* while many others are found largely in the canyons. *Juniperus monosperma* and *J. pachyphloea* occur on the dry slopes and basins, while *J. flaccida* is found most commonly along canyon waterways. The pine of the mountain slopes and basins is the Mexican pinyon (*Pinus cembroides*). Around 5,000 feet elevation, madrona (*Arbutus texana*) is present in this association, while a small group of *Acer grandidentata* grows about 6,000 feet on the slope of Emory peak. *Quercus chisosensis, Q. endemica, Prunus virens, Diospyros texana, Rhus* sp., *Juglans rupestris, Salix goodingii, Celtis laevigata, Morus microphylla,* and *Cercis reniformis* are more likely to be found in canyons than on the dry slopes of the mountain and mesa areas of the Chisos.

Ground cover, in these high mountains and mesa regions, is fairly abundant. Numerous grasses, such as *Muhlenbergia emersleyi, M. rigida, M. pauciflora, Bouteloua gracilis, B. hirsuta, B. curtipendula, B. uniflora, Andropogon saccharoides,* and *Lycurus phleoides,* grow well where the groves of trees do not shut out the sunlight. *Nolina erumpens* forms huge grasslike clumps and is common between 5,000 and 7,000 feet. *Dasylerion leiophyllum* and *Agave lecheguilla* are found as high as 5,000 feet in the more open and dry parts of the community. The frequent, large agave of the Chisos Mountains is *Agave scabra,* a conspicuous member of the Basin vegetation at 5,000 feet. The shrubby growth consists, largely of *Rhus virens, R. microphylla, Cercocarpus eximius, Fraxinus greggii, Acacia constricta, Viquieria stenoloba,* and *Opuntia lindheimeri.*

The mixture of brush and open cover in the pinyon-oak-juniper association is conducive to a varied and rich population of mammals. Many of these mammals are ungulates and carnivores, adapted to the cold temperatures of this high altitude. The white-tailed deer and the squirrels are the most conspicuous members of the association. Antelope squirrels are more abundant here than in other associations. These squirrels were seen, on several occasions, to take seeds from the large opuntias. The brush mouse, encinal mouse, and mountain cottontail are not found on the arid lower slopes of the Chisos. The ringtail cat, rock squirrel, and the skunks are frequent inhabitants of the canyons of this association where there is much exposed rock and sometimes open water.

The large carnivores, the cougar and the bobcat, are well established in the high parts of the Chisos. The bobcat, as evinced by the carcases hung on fences by government trappers, is a more common inhabitant of the desert plains. The cougar, when not frequenting the high mountains, hunts along the Rio Grande river-bottom associations, especially where mesas and mountains lie close to the river's edge.

Yellow-Pine-Fir association

Petran montane Forest Weaver and Clements (1929); *Yellow-pine-juniper* Blair (1940).

Citellus variegatus couchii, Rock squirrel .... Sight
Citellus interpres, Texas antelope squirrel .... Sight
Odocoileus hemionus crooki, Mule deer .... Sight

The yellow-pine-fir association is found in lower Juniper Canyon and in Pine Canyon on the southern edge of the Chisos Mountains. The most outstanding dominant is the yellow pine (*Pinus ponderosa*), while the Douglas fir (*Pseudostuga taxifolia*) is scattered over the canyon floors and slopes. Muller (1937) lists *Quercus chisosensis, Prunus virens, Arbutus texanus, Stipa tenuissima, Bromus marginatus, Poa involuta, Panicum bulbosum, Oryzopsis fimbriata,* and *Muhlenbergia pauciflora* as present in this association. In the Davis and Glass Mountains the only dominant of this association which is present is *Pinus ponderosa.* In these mountains it occurs on north slopes at 6,000 feet elevation.

There was little opportunity to study this association, but some sight records of the larger mammals were secured. Further investigation will probably reveal an interesting assemblage of small mammals, since the grass cover is fairly abundant and there is a good interspersion of open and brushy areas.

Grama-Bluestem association

Roughland-grassland of relatively thick cover of grasses Carter and Cory (1932); *Grama-bluestem association* Blair (1940).

Reithrodontomys fulvescens canus, Fulvous harvest mouse 2
Sigmodon ochragnathus, Mountain cotton rat 8
Odocoileus hemionus crooki, Mule deer .... Sight

In the Chisos Mountains, areas of grassland occur up to 6,000 feet. Grasses typical of fairly mesophytic conditions are often present in these situations. According to Carter and Cory (1932), these grasses include *Stipa tenuissima, Bouteloua curtipendula, Andropogon saccharoides, Heteropogon contortus,* and *Trichachne californica.* The common short grasses are *Bouteloua hirsuta, B. eriopoda* and *B. gracilis.* Oaks, including *Quercus emoryi, Q. grisea,* and *Q. chisosensis,* form "savannahs" around the periphery.

The grama-bluestem association, in the Chisos Mountains, grows on loams and silty loam soils with a 6.6 to 6.7 pH range. The soil is hard packed.

The mammals which are most characteristic of the grama-bluestem association in the Chisos Mountains are the harvest mouse and the cotton rat. One of these grassy areas was used by mule deer for bedding down at night.

Feathergrass-Grama association

Sigmodon ochragnathus, Mountain cotton rat .... Reported*
Odocoileus virginianus carminis, White-tailed deer .... Sight

Laguna is a rich grass area, dominated by species of *Stipa* and *Bouteloua.* Pines and oaks invade the grass along the edge. The grasses are knee deep in places and the whole community presents the aspect of a mixed prairie association. According to Sperry (1938), the grass species are *Stipa eminens, S. neomexicana, S. tenuissima, Bouteloua gracilis, B. hirsuta, Muhlenbergia glauca, M. repens, M. rigida, Panicum obtusum, Bromus anomalus, Eragrostis diffusa, Sitanion hystrix, Lycurus phleoides,* and *Agropyron smithii.*

No traps were set in this association because of lack of transportation. The cotton rat is common, but what other small mammals are present is not known.

* Borell and Bryant, 1942.

DAVIS MOUNTAIN BIOTIC DISTRICT

The Davis Mountain biotic district of the Chihuahuan biotic province was named and described by Blair (1940). Its major divisions are a "Plains life belt" and a "Roughland life belt."

The part of the Davis Mountains, which extends into Brewster County, consists of a long, dissected plateau of igneous rock around Alpine and along the west of the Del Norte Mountains. The northern portion of this plateau is broken into low hills and mesas, many with their axes running north and south. The southern portion, along the Del Norte Mountains, alternates between rolling dissected hills, and block mountains like Elephant, Goat, and Cathedral.

The eastern edge of the Del Norte Mountains, rising to 6,750 feet at Mount Ord, consists of a long, narrow limestone ridge which appears to be a northwesterly extension of the Santiago Mountains. The Glass Mountains, with an elevation of 6,286 feet at Old Blue Mountain, trend northeast-southwest and form the northern boundary of the Marathon Basin. These mountains are composed of Paleozoic limestones and sandstones which are older than those of the Edwards Plateau. On the southwestern and western edges of the Glass Mountains there are numerous, low, limestone hills on which erosion has cut back successive strata to form rock terraces.

The Pecos Plain is the largest basin of the eastern, lowland groups and extends for many miles to the north and northeast of the Davis and Glass Mountains. This large basin is connected by a narrow strip, near Alpine, Texas, to the more southern Marathon Basin which then stretches southward into the Maravillas Valley lowland and the Stillwell Basin. The Pecos Plain and the northern part of the Marathon Basin are fairly level and the soils are generally fine grained. Low hills of Paleozoic chert interrupt the southern part of the Marathon Basin and trend northeast-southwest. The geology of the Marathon Basin is described by King (1937).

The soils of the Davis Mountain biotic district are predominantly of the Reagan, Brewster and Ector series, with a few areas of Toyah soils, as along Limpia creek.

The basins of northern Brewster County are occupied largely by soils of the Reagan series. These soils have more organic material than those of the Reeves series and often support a good grass growth with few shrubs. The short-grass, short-grass-yucca, short-grass-sacahuiste, and short-grass-cholla associations are found on these soils. The reaction ranges from acid in sandy loams to basic in silt and clay loams.

The Ector soils of the north are darker and probably contain more organic material than those of the Chisos biotic district. They were analyzed as silt loam (pH 8.3-8.9), clay loam (pH 8.0-8.7), loam (pH 8.0-8.6), and sandy loam (pH 9). These soils support pinyon-oak-juniper, oak chaparral, juniper-ocotillo, sotol-juniper-lecheguilla, and short-grass-juniper associations.

The igneous soils of the mountainous areas of the Davis Mountain biotic district are similar to those of the Chisos biotic district. In the north they support the yellow-pine-juniper, pinyon-oak-juniper, oak-juniper, short-grass-juniper, and rock-hill associations.

Climatic information for the Davis Mountain biotic district is good as far

as the western portion is concerned. Fairly consistent records have been taken at Mount Locke, Fort Davis and Alpine, Texas, for the last twenty years. There is no available record of the climatic information for the Marathon Basin or the Glass Mountains on the east. The average yearly temperature in the Davis Mountains is 50 degrees with an extreme range of -3 to 108 degrees for the years 1929 to 1948. Alpine, Texas, just south of the Davis Mountains in the plains life belt of the Davis Mountain biotic district, gives for the same years an average of 62 degrees with an extreme range of -2 to 106 degrees. The median for total precipitation at Fort Davis for the years 1929 to 1948 is about 15 inches while the median for Alpine for the same years is about 13 inches. The total rainfall for Fort Stockton in the Pecos Plain, for these years, is close to that for Alpine, but the mean temperatures at Fort Stockton are, with very few exceptions, higher than those at Alpine.

PLAINS LIFE BELT

This life belt, in northern Brewster County, is found from 4,000 to 5,000 feet elevation and includes the short-grass, short-grass-yucca, short-grass-cholla, short-grass sacahuiste, huisache, river walnut, and juniper-ocotillo associations. The soils belong to the Reagan series and are usually hard packed with considerable gravelly material. The climatic data for Alpine represent the conditions for this life belt.

Short-Grass association

Gramma-grass association Shantz and Zon (1924); *Aristida-bouteloua association* Weaver and Clements (1929); *Short-grass association* Blair (1940).

Citellus spilosoma marginatus, Spotted ground squirrel	4
Cynomys ludovicianus arizonensis, Prairie dog	Sight
Cratogeomys castanops lacrimalis, Plateau pocket gopher	Sight
Perognathus merriami gilvus, Pocket mouse	12
Onychomys torridus torridus, Grasshopper mouse	6
Peromyscus leucopus tornillo, Wood mouse	3
Lepus californicus texianus, Black-tailed jackrabbit	Sight
Sylvilagus audubonii neomexicanus, Audubon cottontail	Sight
Antilocapra americana americana, Pronghorn antelope	Sight

Areas of short-grass, undisturbed by shrub vegetation, are neither extensive nor common in relation to the entire area of the Davis Mountain biotic district. In Brewster County, this association is restricted to a few of the better managed valleys adjacent to or within the mountain areas. The dominant grasses are *Bouteloua gracilis, B. hirsuta, B. barbata, B. eriopoda, Aristida purpurea, A. glauca, A. pansa, A. wrightii,* and *A. adscencionis*. Some of the other grasses which may be present in the association are *Bouteloua curtipendula, Eragrostis intermedia, Muhlenbergia arenacea, M. arenicola,* and *Sitanion hystrix*. In many areas evidence of overgrazing was obvious, through the sparse and irregular occurrence of shrubs like *Prosopis glandulosa, Microrhamnus ericoides, Juniperus monosperma,* and the three-awns (*Aristida* sp.). The soils are sandy loams (pH 7.0), silt loams (pH 6.73), and clay loams (pH 8.25). The soils of this association have been packed hard by the trampling of cattle.

Several trapping areas in the short-grass association are badly over-grazed, the grass being less than one inch high. In these areas only the pocket mouse

was caught. Only two situations presented a good growth of short grasses and it was in these that the grasshopper mice, wood mice, and the ground squirrels were secured. At one trapping location two immature *Citellus spilosoma* were taken at one time in the same museum special trap. Pocket-gopher mounds were most abundant wherever the association bordered a highway. An individual of this large pocket gopher was observed beside its mound one afternoon. Signs of a large prairie-dog colony were seen near the Hess ranch, Glass mountains, at 4,600 feet elevation. An active colony, about four acres in extent, was observed one mile west of Alpine. There were mounds about every twenty feet and there appeared to be an average of two dogs to a burrow. The cottontail is not abundant in this association. The two species of harvest mouse (*Reithrodontomys montanus griseus* and *R. megalotis megalotis*) and the deer mouse (*Peromyscus maniculatus blandus*), caught in this association by Blair (1940), were not present in these trapping samples.

Short-Grass-Yucca association

Black grama Shantz and Zon (1924); *Desert plains grassland* Weaver and Clements (1929); *Short-grass yucca association* Blair (1940).

Citellus mexicanus parvidens, Mexican ground squirrel	1
Citellus spilosoma marginatus, Spotted ground squirrel	Sight
Cratogeomys castanops lacrimalis, Plateau pocket gopher	Signs
Perognathus merriami gilvus, Merriam pocket mouse	17
Perognathus hispidus paradoxus, Plains pocket mouse	1
Onychomys torridus torridus, Grasshopper mouse	1
Reithrodontomys megalotis megalotis, Desert harvest mouse	1
Peromyscus pectoralis laceianus, Encinal mouse	2
Lepus californicus texianus, Black-tailed jackrabbit	Sight
Sylvilagus audubonii neomexicanus, Audubon cottontail	Sight
Antilocapra americana americana, Pronghorn antelope	Sight

One of the most extensive grass communities of the Davis Mountain district is typified by various species of *Yucca*. The most extensive areas are the Marfa Plateau and the northern part of the Marathon Basin. Smaller areas of this association are found around Alpine, Brewster County. Gentle slopes, which are not overgrazed, often support a short-grass-yucca association, but the common yucca, in this instance, is *Y. torreyi*, whereas the plains are dominated by the two smaller species, *Y. elata*, and *Y. thompsoniana*. The grasses include those found in the short-grass association, but there is a better growth of *Bouteloua curtipendula*, *Muhlenbergia* sp., *Aristida ternipes*, *Eragrostis* sp., and *Andropogon* sp. The shrubs, *Koeberlinia spinosa*, *Microrhamnus ericoides*, *Berberis trifoliata*, *Ephedra* sp., *Acacia greggii*, and *A. constricta* are frequent. The soils found in this association are silt loam (pH 8.5) and loam (pH 8.6).

This association is more productive in species of mammals than the short-grass and short-grass-sacahuiste associations. Both species of spermophile are recorded from this association, but *Citellus mexicanus parvidens* is more typical of the tobosa associations. The cottontail is abundant, possibly, as suggested by Blair (1940), because of greater cover beneath the shrubs. Jack rabbits were common in this association during the spring of 1947 but decreased in number greatly by 1948. Antelope are kept by several ranchers and confine themselves almost entirely to the short-grass, short-grass-yucca, and short-grass-sacahuiste associations.

Short-Grass-Cholla association

Triodia-scleropogon association Warnock (1946); Unpublished Ph.D. dissertation, University of Texas.

Onychomys torridus torridus, Grasshopper mouse	6
Cynomys ludovicianus arizonensis, Prairie dog	Signs
Perognathus merriami gilvus, Merriam pocket mouse	3
Peromyscus leucopus tornillo, Wood mouse	2

This association occurs in small patches in the plains life belt. The most conspicuous member is the arborescent cactus, *Opuntia imbricata,* locally known as "cholla." The most extensive area of this association occurs in Jeff Davis County along the road to Kent. The whole association is very open, the grasses low, and the cholla offers little shelter. The associated plants are *Dyssodia* sp., *Eriogonum wrightii, Porlieria angustifolia, Senecio* sp., *Bouteloua gracilis, Aristida glauca, Scleropogon brevifolius* and *Triodia pulchella.* The soil is clay with an 8.5 pH.

Evidences of a prairie-dog colony were present in this association on the Kuntz ranch. The animals had been removed the previous year. Grasshopper mice are as abundant as in the huisache association but the Merriam pocket mouse is less abundant than on the sandy loam soil of the huisache association.

Short-Grass-Sacahuiste association

Bear grass society Cottle (1931).

Citellus spilosoma marginatus, Plains ground squirrel	Sight
Perognathus merriami gilvus, Merriam pocket mouse	3
Peromyscus eremicus eremicus, Cactus mouse	1
Reithrodontomys megalotis megalotis, Desert harvest mouse	2
Reithrodontomys fulvescens fulvescens, Fulvous harvest mouse	1
Lepus californicus texianus, Black-tailed jackrabbit	Sight
Sylvilagus auduboni neomexicanus, Audubon cottontail	Sight
Antilocapra americana americana, Pronghorn antelope	Sight
Bison bison, Plains bison	Sight

Large areas of the grassland are covered by an association of short grasses and sacahuiste. The association has a very regular pattern and is little disturbed by invading shrubs. The greatest extent of the association occurs between Marfa and the Chinati Mountains in Presidio County but several lesser areas are present in Brewster County. The grasses are *Bouteloua curtipendula, B. hirsuta, B. eriopoda, Aristida purpurea, A. adscencionis, Andropogon scoparius, A. barbinodis, Muhlenbergia arenicola, Hilaria berlangeri,* and *Lycurus phleoides.* This grassland is abundantly dotted with low, regular clumps of *Nolina texana.* The soils are fine sandy loam and clay loam, often containing considerable gravel. A pH of 8.5 was obtained from two samples.

Very few mammals were caught in the short-grass-sacahuiste association. The ground squirrel was not common and the hard soil may account for the paucity of Merriam pocket mice. This harvest mouse (*Reithrodontomys m. megalotis*) does not distinguish any association, since it is widely distributed both in the Plains life belt and the Roughland life belt of Blair (1940). Antelope are more abundant in the other short-grass associations, but a small, introduced herd of bison was seen most frequently in this association.

Huisache association

Perognathus merriami gilvus, Merriam pocket mouse	9
Onychomys torridus torridus, Grasshopper mouse	5
Peromyscus leucopus tornillo, Wood mouse	3

An area of sandy loam with a pH of 8.6 near the Del Norte Mountains supports an association dominated by *Acacia constricta*. This acacia is tall and slender, unlike the bushy habit of *A. greggii*, which forms the "catclaw association" of Blair (1940). The grass cover is very low and sparse, consisting mainly of *Triodia* sp.

The pocket mouse is numerous here, possibly because the surrounding association of short grasses and bear grass grows on a harder soil. Grasshopper mice are abundant compared to the number of other associations and are probably influenced by the open, overgrazed nature of the grass cover. The wood mouse, in this region, is usually found in grass associations heavily dominated by shrubs.

River-Walnut association

Peromyscus boylii attwateri, Brush mouse	4

One of the most distinctive associations of the grassland region is the narrow, streambed community of *Juglans rupestris*. A solid growth of river-walnut trees forms a canopy, twenty to thirty feet high, over the coarse sand and gravel of the dry streambed. *Berberis trifoliata* is usually present and the sparse ground cover consists of *Acalypha neomexicana*, *Croton* sp., *Rivinia* sp., and several other small herbs. The sandy soil of the streambed is easy to dig but unstable due to frequent flooding.

The only mammal trapped in this association was the brush mouse. This mouse is otherwise severely restricted to associations on steep hillsides.

Apache-Plume association

Reithrodontomys fulvescens fulvescens, Fulvous harvest mouse	1

In the gentle draws of the Plains life belt and in the Glass Mountains near 4,500 feet elevation, *Fallugia pardoxa* grows with *Microrhamnus ericoides* and sometimes a fairly good grass cover. The soils are sandy loams and the association never covers an extensive area in any one place.

The only mammal trapped in this association was the harvest mouse. Since the association is not extensive anywhere the harvest mouse may simply be a transient.

ROUGHLAND LIFE BELT

This life belt is recognized in northern Brewster County as occurring above 5,000 feet as described by Blair (1940). The soils belong to the Brewster (igneous) and the Ector (limestone) series and the mother rock is close to the surface. Climatic data for Fort Davis in the Davis Mountains have been given to represent the higher altitudes of this life belt.

Rock-Hill association

Perognathus nelsoni canescens, Nelson pocket mouse	1
Peromyscus boylii attwateri, Brush mouse	3
Peromyscus pectoralis laceianus, Encinal mouse	12

Certain igneous hills east of Alpine, Brewster County, are almost bare of vegetation. The surface is very irregular and consists of large, angular blocks

of talus. The slope is abrupt, about 50 degrees from the horizontal, and the long axis trends north and south. The soil from one hill is a loam (pH 8.5), and from the second hill a silt loam (pH 7.2). Even the crevices of soil have been packed hard from the trampling by sheep and cattle.

According to Dr. B. H. Warnock of Sul Ross State Teachers College, Alpine, these hills were once covered by a short-grass-yucca stand, but have been severely overgrazed for several years. Because of this latent potentiality to support a short-grass-yucca association, the rock-hill association is included in the Davis Mountain Biotic district. Ground cover is supplied by the talus blocks and by scattered tufts of grass, largely *Bouteloua hirsuta* and *Aristida glauca*. There is practically no crown cover.

The mammals are predominantly saxicolous forms common in the north. This is the only association, in the north, where a specimen of the Nelson pocket mouse was secured.

Juniper-Ocotillo association

Perognathus merriami gilvus, Merriam pocket mouse	6
Perognathus hispidus paradoxus, Plains pocket mouse	1
Peromyscus maniculatus blandus, Deer mouse	1
Peromyscus leucopus tornillo, Wood mouse	3
Peromyscus eremicus eremicus, Cactus mouse	4

On certain, low, limestone hills west of the Glass Mountains, an association distinguished by *Fouquieria splendens* and *Juniperus monosperma* occurs. The sparse soil is a clay loam with an 8.6 pH. The accompanying shrubs are xeric in nature, including *Microrhamnus ericoides, Acacia* sp., *Mimosa* sp., and *Dalea* sp. The sparse ground cover consists of *Selaginella rupestris, Bouteloua gracilis, Aristida glauca,* and *Triodia pulchella.*

As would be expected from the heterogeneous nature of this association, the mammalian members are a mixture of the desert, grassland, and woodland species in this region. The Merriam pocket mouse and the cactus mouse are common to many arid associations. The plains pocket mouse and the deer mouse are more typical of grassland associations. The wood mouse is found in several life belts of the region and is most common in brushy habitats.

Sotol-Juniper-Lecheguilla association

Canis latrans, Coyote	Reported
Lynx rufus baileyi, Bobcat	Reported
Perognathus merriami gilvus, Merriam pocket mouse	1
Peromyscus leucopus tornillo, Wood mouse	1
Peromyscus pectoralis laceianus, Encinal mouse	32

The lower limestone slopes and outlying hills of the Glass Mountains from 4,000 to 5,000 feet elevation support a distinctive association. Soil is scarce and the dry conditions of these hills favor the growth of desert plants such as ocotillo, acacia, sotol, and lecheguilla. Other plants, such as the low oaks, junipers, and grasses, have been derived from the woodland and grassland formations, so that this is not a typical desert association. Some of the associated plants are *Quercus* sp., *Juniperus monosperma, Rhus* sp., *Acacia greggii, Krameria grayii, Nolina texana, Bouteloua hirsuta, B. curtipendula, Aristida glauca,* and *Stipa tenuissima.*

The soils of this association are silt loam (pH 8.3-8.9) and loam (pH 8.0). The cover is good considering the arid nature of the habitat.

Encinal mice can be said to typify this mixed association. These mice are abundant as compared to their numbers in many associations. The sotol-juniper-lecheguilla association, in the Glass Mountain, is a favored area of the domestic sheep and goats and the ranchers reported the presence, here, of the coyote and bobcat. Several dead sheep and goats were observed, but there were no signs of predation. Many of the northwest slopes of the Glass Mountains are so badly overgrazed that only a few scattered plants remain and even the sotol is cut for fodder.

Juniper-Sacahuiste association

Perognathus merriami gilvus, Merriam pocket mouse	11
Dipodomys merriami ambiguus, Merriam kangaroo rat	1
Peromyscus pectoralis laceianus, Encinal mouse	1
Lepus californicus texianus, Black-tailed jackrabbit	Sight
Sylvilagus audubonii, Audubon cottontail	Sight

One of the most unusual associations of the Glass Mountains is that dominated by low spreading junipers and large clumps of sacahuiste. The association is found on gentle slopes from 4,000 to 4,600 feet elevation. The junipers and sacahuiste are regularly spaced about for or five feet apart and there is little ground cover other than these plants. Other plants include *Pinus cembroides, Berberis trifoliata, Krameria grayii, Aristida barbata,* and *Triodia* sp. The soil is a clay loam (pH 8.4) with many pebbles and is similar to that found in the creosote associations of the desert plains.

With an open, arid nature and such a soil texture, it is not surprising to find this association characterized by a kangaroo rat and the Merriam pocket mouse. Soil is possibly more influential in the distribution of this pocket mouse and kangaroo rat than altitude.

Short-Grass-Juniper association

Citellus mexicanus parvidens, Mexican ground squirrel	1
Citellus spilosoma marginatus, Plains ground squirrel	1
Perognathus merriami gilvus, Merriam pocket mouse	5
Perognathus hispidus paradoxus, Plains pocket mouse	1
Reithrodontomys megalotis megalotis, Harvest mouse	1
Peromyscus leucopus tornillo, Wood mouse	3
Peromyscus boylii attwateri, Brush mouse	1
Peromyscus pectoralis laceianus, Encinal mouse	31
Antilocapra americana americana, Pronghorn antelope	Sight

A community, dominated almost entirely by *Juniperus monosperma* and species of *Bouteloua* and*Aristida,* is very noticeable throughout the grassland of the Big Bend. The invasion of juniper into former grassland, in highland areas, is a result of overgrazing, which breaks the compact sod of short grasses and allows the juniper seedlings to obtain a foothold. The area occupied by this disclimax has increased considerably within late years (Bell and Dyksterhuis, 1943). This association possesses characteristics typical of both the adjacent woodland and grassland formations. The junipers are regularly spaced about six feet apart and interpersed with the shrubs *Dasylerion leiophyllum, Acacia greggii, Mimosa dasyacarpa,* and *Opuntia imbricata.* The common grasses are *Bouteloua hirsuta, B. gracilis, B. chondrosoides, Aristida glauca, A. barbata,* and *Eragrostis intermedia.* The soils are clay loams, silt loams, and loams, with a range of 6.3 to 8.7 in pH. All these soils are hard and rocky.

The short-grass-juniper association usually borders an oak-juniper association found on broken rock outcrops in the Big Bend region. The encinal mouse is more typical of the short-grass-juniper association, while the brush mouse, common in the oak-juniper, is seldom taken in this association. The plains pocket mouse (*Perognathus hispidus paradoxus*) is largely confined to such open associations with hard soils. The wood mouse is also typical of open, shrub invaded grassland in the Big Bend region.

Oak Chaparral association

Chaparral division Shantz and Zon (1924); *Petran chaparral subclimax* Weaver and Clements (1929); *Cercocarpus-quercus association* Warnock (1946).

Peromyscus pectoralis laceianus mouse	4
Sylvilagus audubonii, Audubon cottontail	Sight
Odocoileus hemionus crooki, Mule deer	Sight

Of two areas of oak chaparral on the west side of the Glass Mountains at 5,000 feet elevation, only one was trapped. The low oaks were mostly *Quercus mohriana* accompanied by *Cercocarpus breviflorus, Juniperus monosperma* and *Nolina texana. Croton corymbulosus* was common throughout this association and the only identifiable grass was *Aristida adscencionis*. The soil is a loam (pH 8.6). The cover is more open than in the chaparral of the Chisos Mountains.

As in the Chisos Mountains, the common, small mammal is the encinal mouse. The low oaks offer good cover for the cottontail. Mule deer were seen in this association on several trips through the mountains.

Oak-Juniper association

Quercus-juniperus Weaver and Clements (1929); *Oak-juniper association* Blair (1940); *Quercus-juniperus association* Warnock (1946).

Procyon lotor fuscipes, Raccoon	Sight
Bassariscus astutus flavus, Ringtail cat	Sight
Urocyon cinereoargenteus scottii, Gray fox	Sight
Citellus variegatus couchii, Rock squirrel	Sight
Perognathus merriami gilvus, Merriam pocket mouse	3
Peroymscus boylii attwateri, Brush mouse	25
Peromyscus pectoralis laceinaus, Encinal mouse	15
Odocoileus hemionus crooki, Mule deer	Sight

The most common community of the woodland climax, in the Big Bend, is the oak-juniper association, which ranges from 4,500 to 6,000 feet, depending on the slope. This community is found in all the higher mountains, many of the lower ones, and even as the dominant vegetation of some of the higher mesas, such as Nine-Point mesa in Brewster County. The association is typical of igneous masses and is described as occurring from 4,500 to 6,000 feet in the Chinati Mountains (Tinkham, 1948), from 5,000 to 6,000 feet in the Davis Mountains (Blair, 1940), and, from the very highest points of the Sierra Tierra Vieja (Hinckley, 1947). This community is also found on low, igneous hills and outcrops throughout the grassland of the northern Big Bend, where it forms sharp ecotones with the various grassland communities.

The oaks of the oak-juniper association are *Quercus grisea, Q. emoryi,* and *Q. gravesii.* These three oaks are co-dominant with *Juniperus monosperma.* The shrub associates are *Cercocarpus breviflorus, Acacia texensis, Acacia*

greggii, and *Rhus* sp. The grasses are *Bouteloua gracilis, B. hirsuta, B. curtipendula, B. chondrosoides, Muhlenbergia emersleyi, Erogrostis intermedia, Andropogon barbinodis, Aristida purpurea, A. barbata*, and *A. adscencionis*.

The soils are fine sandy loams and loams with a range of 6.1 to 8.2 in pH. The ground is rocky with pockets of soil.

The mammals most typical of this association are the brush mouse and the encinal mouse. The ringtail and the rock squirrel are usually associated with rocky outcrops, such as the oak-juniper association occupies. A gray fox den was found and the female observed several times in an oak-juniper stand in Sunny Glenn. The raccoon was flattened on the highway near Paisano Pass, and is assigned to the subspecies *fuscipes* according to Blair (1940).

Pinyon-Junper association

Pinyon-juniper Shantz and Zon (1924); *Pinus-juniperus* Weaver and Clements (1929); *Pinyon-juniper association* (1940); *Pinus cembroides association* Warnock (1946).

Perognathus merriami gilvus, Merriam pocket mouse	2
Peromyscus pectoralis laceianus, Encinal mouse	23

The pinyon-juniper association was studied only in the Glass Mountains and occurred there and in the Del Nortes above 5,500 feet elevation. The stands of pinyon and juniper in the Glass Mountains are open and the juniper gives the greatest amount of cover. Associated plants are few and include *Quercus mohriana, Agave lecheguilla*, and *Aristida* sp. The soils are sandy loam and loam with a range of 8.3 to 9.0 in pH.

In the Glass Mountains, at least, this is an unproductive association as far as variety of mammals is concerned. The associations of these mountains are mostly of a xeric character compared to many in the Davis and Del Norte mountains. The most typical small mammal of this association is the encinal mouse.

Biotic Position of Brewster County

The inclusion of the Big Bend region of Texas within the Chihuahuan biotic province has been established by Blair (1940) and Dice (1943), but the differentiation between the northern grassland area of the Big Bend and the southern shrub area, which extends south into Coahuila and Chihuahua, is more difficult to establish. Studies of the avian and reptilian faunas of the Big Bend have not been, until very recently, of a nature to aid in the solution of this problem. Although extensive collections of mammals have been made in the Davis Mountains by Blair (*loc. cit.*) and in the Big National Park by Borell and Bryant (1942), there are several mammalian forms whose taxonomic status remains doubtful. The Merriam pocket mouse (*Perognathus merriami gilvus*) from the southern part of the Big Bend, for example, is difficult to fit within the subspecies *gilvus* and yet it does not seem sufficiently differentiated to warrant a new category. The taxonomic status of the cottontails of the region is uncertain and there are questions, unanswered at present, regarding the subspecies of *Peromyscus boylii* and *P. leucopus* which occur in several parts of the Big Bend region. A new subspecies of *Dipodomys merriami* has been described by Blair (1949) from Presidio County, but the full extent of its range is not yet known. The taxonomic status of *Perognathus nelsoni*

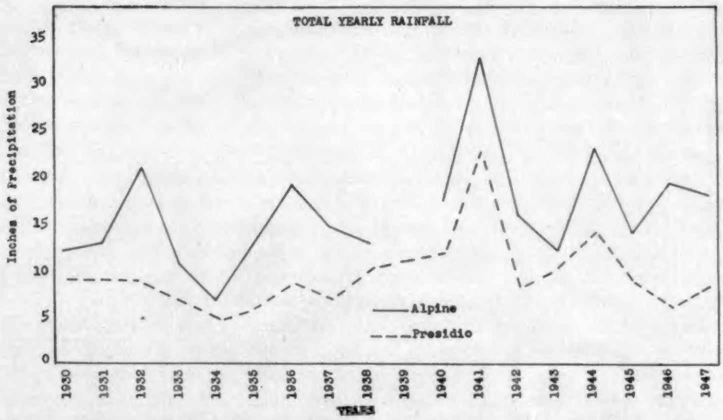

Fig. 2.—Total yearly rainfall at Alpine in northern Brewster County compared to the total yearly fall for Presidio in southern Presidio County.

canescens in this region is also in dispute (Blair, 1938), (Borell and Bryant, 1942).

On the basis of the investigations of the Davis Mountain region by Blair (*loc. cit.*) and the southern part of Brewster County by Borell and Bryant (*loc. cit.*), there are, at present, sixty-seven species with a total of seventy-five subspecies of mammals recognized for Brewster and Jeff Davis counties, Texas. Of these mammalian forms, thirty-three subspecies are common to both the Chisos and Davis Mountain biotic districts. Of the twelve, different species of bats, six are found only in the Chisos biotic districts and one species only in the Davis Mountain biotic district. Of the sixty-seven, mammalian, terrestrial species, thirteen are found in the Davis Mountain biotic district and not in the Chisos biotic district, whereas seven species recorded for the Chisos biotic district have not been found in the Davis Mountain biotic district.

The differentiation of the Chisos biotic district from the Davis Mountain biotic district within the Big Bend of Texas is further supported by climatic and edaphic factors. Both total, and maximum and minimum rainfall, as well as maximum and minimum temperatures, show considerable and fairly consistent differences between northern and southern Brewster County, as represented by the stations at Alpine and Presidio (figs. 2, 3).

The edaphic differences are also striking. The soils of the Plains Life belt of the Davis Mountain biotic district belong, largely, to the Reagan and Toyah series, those of the Desert plains life belt of the Chisos biotic district to the Reeves, Gila, Rio Grande, and Anthony series, while the large tobosa transitions occupy soils of the Verhalen series and, occasionally, the silty clay loams of the Reeves series.

Since both districts lie within the Chihuahuan biotic province, many of the same plant species are shared, but the various assemblages of these species differ considerably between the two, designated biotic districts. The woodland

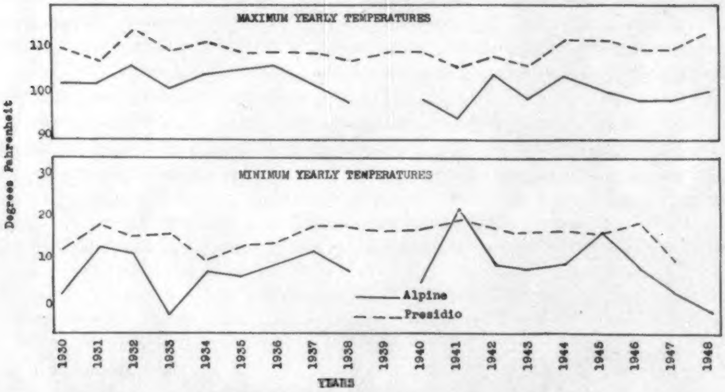

Fig. 3.—Maximum and minimum yearly temperatures for Alpine in northern Brewster County compared with those for Presidio in southern Presidio County.

association of oak and juniper is common to both biotic districts. In the Davis Mountain biotic district, however, it is a conspicuous community occupying the frequent outcrops, hills and mountains, while in the Chisos biotic district this association is found only on the higher igneous mountains and mesas. Furthermore, there are differences in the associated plant species in this association between the two biotic districts. On the other hand, a distinctive association of sotol and lecheguilla covers large areas throughout the Chisos biotic district, whereas any community in the Davis Mountain district, bearing similarity to the sotol-lecheguilla association, is found on limestone only, and is modified by the presence of certain plant species from the woodland communities. There are few areas in the Chisos biotic district which bear any resemblance to the extensive short-grass-yucca and short-grass- sacahuiste associations which typify the ecologic picture of the Plains life belt of the Davis Mountain biotic district. The presence of certain, small areas of creosote within the grassland of the North is simply an invasion, due to poor land management, by communities which cover vast lowland areas within the Chisos district. Lastly, the assemblages of mammals occupying these different associations make it apparent that there is strong evidence for the differentiation of the two biotic districts on the basis of ecologic associations alone.

The higher mountains of the Davis Mountain and Chisos biotic districts present problems in the disjunct distribution of ecologic associations. The question then arises of a designation of separate biotic districts for these distinct mountain systems. The communities of the Glass Mountains are influenced by the limestone substrata and are therefore not totally similar to the communities of the Davis Mountains. There is not, at present, sufficient biotic information on which to designate a distinct biotic district for the Glass Mountains.

Since the Chisos Mountains support ecologic associations differing greatly from those of the surrounding desert plains there is some basis for distinguish-

ing a Chisos Mountain biotic district. There is, however, biotic continuity between the surrounding plains and the mountains. Furthermore, should such a distinction be made between the Chisos Mountains and the surrounding desert plains it would then become necessary to distinguish every high, desert mountain system in the Chihuahuan biotic province as a separate biotic district.

Many square miles of the Chihuahuan biotic province are transitional in character and present an intersperion of associations representing elements from the Tamaulipan, Comanchian, Navahonian, and Apachian biotic provinces. Such a diverse area does not fall readily into definite patterns of biotic differentiation, but simply follows the varied influences of exposure, slope, drainage, soil, and altitude; all of which change radically within a few miles. If too great an emphasis is placed upon these abrupt changes, the designation of biotic districts can be carried to extremes. The truly semidesert areas of the central part of the Chihuahuan biotic province appear to form a unity, modified drastically by the abrupt nature of the physical environment, so that certain differences are exaggerated out of proportion to their importance to the ecological picture as a whole. For these reasons, and until further information on climate, animal life, and land misuse is available, only two biotic districts in Brewster County, Texas, other than the Stockton plateau, are recognized.

SUMMARY

That part of Brewster County which possesses true basin and range physiography is included in the Chihuahuan biotic province. It is further subdivided, on the basis of local differences in climate, soils, and ecologic associations, into two biotic districts. In the Chisos biotic district, three life belts and nineteen ecological associations are described. In the Davis Mountain biotic district, two life belts and fifteen ecologic associations occur.

The plant communities of Brewster County are largely edaphically controlled. Altitude, nature of the surface, and degree of slope also modify the distribution of the plant communities.

Much of the Chihuahuan biotic province is transitional in character. There are many radical changes in exposure, slope, drainage, soil, and altitude which cause great variations in the vegetational patterns. The tendency to designate each different area, such as separate mountains, as distinct biotic districts should be avoided in order not to minimize the essential unity of the central part of the Chihuahuan biotic province.

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Relative Toxicity of Certain Chemical Agents at Low and Room Temperature in a Homeotherm (Mouse) and a Poikilotherm (Frog)

William A. Hiestand, Fred W. Stemler and Ruth F. Madden[1]

Purdue University, Lafayette, Indiana

Measurements of drug toxicity in relation to temperature have been undertaken by many investigators almost since the beginning of pharmacology. Drug toxicity has been considered from the aspect of body and ambient temperatures. For an excellent review of the effect of body temperature on drug action the reader is referred to Fuhrman (1946). The references used in the present communication are specifically those applying to identical chemical agents or ones having similar effects. With warm-blooded animals drugs are usually more toxic at low environmental temperatures and with cold-blooded forms the reverse is usually true. This is undoubtedly due in a measure to the fact that homeothermic animals must maintain a body temperature usually 10 to 20 degrees higher than their ambient temperature and are stressed or abnormally taxed when the environmental temperature is low. Poikilotherms are better able to tolerate low external temperatures as their metabolic rate depends largely upon external heat, therefore the rate of chemical metabolism is increased with rise of external temperature and one would assume toxicity would likewise increase. Some exceptions can be found during hibernation when caffeine and strychnine become more toxic to the ground squirrel at low temperatures (Pfeiffer et al, 1939).

Comparisons of toxicities of drugs to mice and frogs have been recorded. Thus, drugs more toxic to the frog than to the mouse include methylguanidine, synephrine, phenol, caffeine, resorcinol and nupercaine, while acetylcholine, aminopyrine, picrotoxine and sodium cyanide are more toxic to the mouse (Führer, 1932). Epinephrine was found to be 60 times as toxic to the mouse. McGuigan (1938) has stated that the fatal dose of digitalis is 6 times as great for the frog as for the dog. Reduction of strychnine convulsions in frogs by reducing the external temperature has been reported (Kunde, 1860; Githens, 1913; Schlomovitz and Chase, 1916; Lambruschini, 1938; Gast, 1943). Others have studied reduced toxicity of other drugs to frogs at low temperatures (Herrmann, 1941; Fuhrman et al, 1943; Sievers and McIntyre, 1937; Sivadjian, 1946; Nedzel, 1951; Richards, 1941). Some drugs have been reported more toxic to frogs at low temperature (Richards, 1941; Gunther and Odoris, 1944). Such is true of barbiturates. Also with homeotherms (rats) pentobarbital proved to be more toxic if the animals were placed in a draft (Cameron, 1939) which agrees with our findings with mice. Hermann (1867) found rabbits more resistant to ethyl alcohol when warmed

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TABLE 1.—Effect of 2 different ambient temperatures on toxicity of certain chemical agents to mice. As soon as each drug was administered intraperitoneally each group of 10 mice was placed in a room of either 22±1° or 2—5°C. Mortality is stated in terms of percentage of mice dead at the end of 24 hours.

Chemical Agent	Dosage	Percent mortality 24 hours at temperature 22±1°	2—5°
		%	%
Insulin	4.6 u/kg	20	20
	9.2 u/kg	50	100
	100 mg/kg	0	0
Atropine SO_4	200 mg/kg	10	90
	400 mg/kg	90	100
Morphine SO_4	50 mg-/kg	0	90
Amphetamine	35 mg/kg	0	0
	100 mg/kg	10	100
	200 mg/kg	100	100
Ethanol 24%	10 ml/kg	0	10
36%	10 ml/kg	0	50
48%	10 ml/kg	0	100
95%	10 ml/kg	80	100
Na-pentobarbital	300 mg/kg	10	100
Na-phenobarbital	300 mg/kg	10	100
Cortisone acetate	100 mg/kg	0	0
Cocaine HCl	20 mg/kg	0	0
	60 mg/kg	20	90
Priscoline	25 mg/kg	0	0
	100 mg/kg	30	100
controls: no medication			
20 mice exposed 48 hrs.		0	0
10 mice exposed 72 hrs.		0	0

than when kept cool. Young animals because of their pokilothermic state are more resistant to chemical toxicity with the exception of the precocious new-born guinea pig (Fazekas et al., 1941; Windle, 1943).

MATERIALS AND METHODS

Only 2 species of animals were used, the adult white mouse as the homeotherm and the grass frog as the poikilotherm. Two temperatures were used, room temperature of 22±1° C and a low temperature of 2-5° C pro-

duced in a refrigerated room. All drugs tried with the mice were injected intraperitoneally, all drugs used with the frogs were injected by way of the thigh into the dorsal lymph sac. As soon as each animal was injected it was either placed in the cold room or left at room temperature. The criterion of toxicity was the number of animals found dead at the end of 24 hours or at other periods of time as so stated. Ten mice and 10 frogs were used

TABLE 2.—Effect of 2 different ambient temperatures on toxicity of certain chemical agents to frogs. As soon as each drug was administered by way of the dorsal lymph sac each group of 10 frogs was placed in a room of 22±1° or 2—5°C. Mortality is stated in terms of per cent of frogs dead at end of 24 hours.

		%	%
		Percent mortality 24 hours at temperature	
Chemical Agent	Dosage	22±1°	2—5°
Insulin	250 u/kg	10	0
	500 u/kg	0	0
	1000 u/kg	30	0
Ethanol 50%	60 ml/kg	0	0
65%	60 ml/kg	90	30
80%	60 ml/kg	100	100
Na-pentobarbital	300 mg/kg	10	0
	500 mg/kg	100	100
	600 mg/kg	70	100
Priscoline	62.5 mg/kg	100	60
Nicotine SO_4	50 mg/kg	100	20
Quinine SO_4	500 mg/kg	100	0
Strychnine SO_4	2 mg/kg	100	0
	5 mg/kg	100	0

in each procedure, 10 at room temperature were thus compared with 10 in the cold, each group receiving the same dose of the chemical agent. Different strengths of some of the drugs were sometimes used when it was found that the first dosage had been too small. In some cases as with strychnine and insulin the frogs were observed on successive days since they showed no effects of toxicity at the low temperature in 24 hours.

RESULTS

The results are shown in tabular form. In all instances the drugs were equally or more toxic to the mice at the lower temperature (table 1). The reverse effects are shown by the frogs (table 2) with the one exception of

Na-pentobarbital in which case 100% died at the cold temperature while only 70% died at room temperature. With as few as 10 mice this may not be a significant difference. However, it has been reported that barbiturates are more toxic to frogs at lower temperatures (Cameron, 1939; Hermann, 1867). Further observation of the frogs after 24 hours showed that all receiving strychnine and kept at the low temperature were dead in 11 days. Likewise frogs receiving insulin and kept in the cold showed 3 dead in 10 days and 7 dead in 17 days. These were frogs receiving the largest dose of 1000 u/kg.

Further study of strychnine toxicity at low temperature in frogs was carried on by determining the length of time necessary to kill frogs with two different doses, one of 5 mg/kg and the other of 2 mg/kg. The results of this experiment are shown in table 3. Following the larger dose all frogs were dead in 12 days; with the smaller dose 4 frogs survived but remained convulsive over a week. The frogs remained motionless in the cold room in a pan but would straighten out with an extensor thrust of the hind legs when the pan was tapped.

TABLE 3.—Survival of frogs at 2—5°C after receiving large doses of strychnine via dorsal lymph sac.

10 frogs receiving 2 mg/kg	10 frogs receiving 5 mg/kg[2]
4 days later 2 dead	6 days later 4 dead
5 days later 3 dead	8 days later 5 dead
6 days later 4 dead	10 days later 8 dead
7 days later 6 dead	12 days later 10 dead
Remaining 4 frogs survived	

[2] 10 other frogs receiving 5 mg/kg kept at 22°C. All dead in 4½ hours.

SUMMARY

A comparison was made of the toxicity of certain drugs on a homeotherm (mouse) and a poikilotherm (frog) at 2 different temperatures, 22° and 2-5°. All compounds were more toxic to frogs at the higher temperature. It was found possible to prevent dying of frogs with massive doses of strychnine if they were kept long enough at low temperature. By contrast, chemical compounds were more toxic to the mice at low temperature.

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The Appendicular Myology of the Pygmy Falcon (Polihierax semitorquatus)

Andrew J. Berger
University of Michigan, Ann Arbor

The African Pygmy Falcons of the genus *Polihiërax*, together with four other genera (*Spiziapteryx, Gampsonyx, Microhierax,* and *Neohierax*), have been placed in the subfamily Polihieracinae (Peters, 1931:281-284). Except for some general comments on *Microhierax* (Beddard, 1898:473-474; Pycraft, 1902:297; Friedmann, 1950:3), apparently nothing has been published on the internal anatomy of these genera. I am indebted to Mr. John G. Williams of the Coryndon Museum, Nairobi, East Africa, for sending me an alcoholic specimen of *Polihiërax semitorquatus,* upon which this paper is based. All dissection was done with the aid of a binocular microscope using 10x magnification. Terminology for wing muscles follows Fisher (1946); that for leg muscles follows Berger (1953).

Wing Myology

I have selected for discussion primarily those muscles which may prove useful in classification or which differ from the general diagnosis for falconiform birds as given by Beddard (1898:472-485) and Friedmann (1950:3, 60-61). The general pattern of the wing myology is closer to that found in certain cuckoos than to that in the Cathartidae (Fisher, 1946); and for muscles not discussed here, it may be assumed that the muscles are similar in origin, insertion, and relative development to the same muscles in *Coua caerulea* (Berger, 1953).

M. pectoralis superficialis appears to be a single muscle, rather than one divided into a superficial and a deep layer as described by Fisher (1946:577) and Beddard (1898:475) for the Cathartidae and other falconiform birds. *M. pectoralis, pars propatagialis,* is a well developed fleshy slip which inserts on the distal end of the belly of *M. tensor patagii brevis.*

M. supracoracoideus arises from the anterior two-thirds of the basal half of the carina and from the adjacent area of the anteromedial surface of the body of the sternum. The total length of the fleshy belly is 30 mm. The course and insertion of the tendon are like those in *Coua.*

M. latissimus dorsi, pars anticus (fig. 1), is a thin strap of muscle arising from the neural spines of the last two cervical (Nos. 14 and 15) and the first dorsal vertebrae. It inserts by a semitendinous band over an area 4 mm wide, beginning 4 mm inferior to the junction of the head of the humerus and the deltoid crest. *Pars posticus* arises entirely from the anterior edge of the pelvis (including the anterior iliac process) and inserts by a small round tendon (less than .5 mm in diameter) on the same ridge as, and immediately

proximal to, the insertion of pars anticus. The dermal component, present in *Coua*, seems to be absent.

M. rhomboideus superficialis (fig. 1) arises from the neural spines of the last three cervical and the first three dorsal vertebrae. It inserts on about the anterior half (15mm) of the dorsomedial surface of the scapula, beginning 3 mm caudal to the tip of the acromion process.

M. rhomboideus profundus (fig. 1) arises from the neural spines of the last two cervical and the first three dorsal vertebrae and inserts on the caudal 12 mm of the dorsomedial surface of the scapula.

M. coracobrachialis anterior arises by a short tendon from the head of the coracoid. The belly is 8 mm long and 3 mm wide at its insertion on the ventral surface of the humerus just proximal to the area of insertion of the pectoralis superficialis on the deltoid crest. The belly is poorly developed and does not cover the anterior surface of the humeral head as in *Coua*.

The common belly of *Mm. tensores patagii longus et brevis* (fig. 1) is 20 mm long and 6 mm in maximum width. The tendon of the tensor patagii longus is similar in structure and insertion to that in *Coua caerulea* (Berger, 1953:57). The tendon of the tensor patagii brevis is formed by two equal components: the one arises at the distal end of the muscular belly; the other from the superficial tendinous envelope which surrounds the insertion of pectoralis superficialis. Part of the tendon of the brevis fuses with a strong tendon on the superficial surface of *M. extensor metacarpi radialis*. The latter tendon attaches proximally to the ectepicondylar process of the humerus and, distal to the area of fusion, fleshy fibers of the extensor metacarpi radialis arise from both the superficial and deep surfaces of this tendon-sheet. The main tendon of brevis, however, continues posteriorly over the forearm muscles for a short distance before it bifurcates. One branch runs proximad to attach

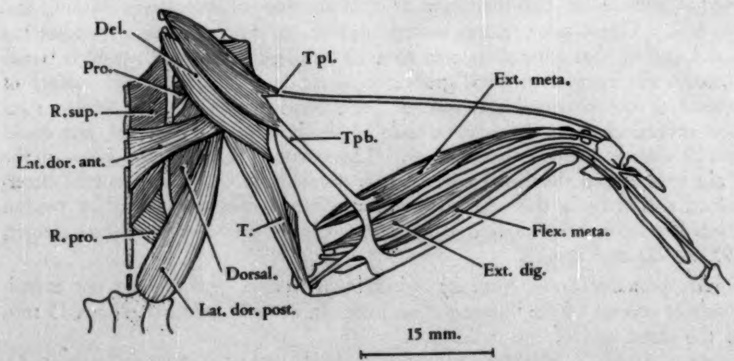

Fig. 1.—*Polihierax semitorquatus*. Superficial muscles of the anconal surface of the right shoulder, arm, and forearm. Del., deltoideus major; Dorsal., dorsalis scapulae; Ext. dig., extensor digitorum communis; Ext. meta., extensor metacarpi radialis; Flex. meta., flexor metacarpi radialis; Lat. dor. ant., latissimus dorsi, pars anticus; Lat. dor. post., latissimus dorsi, pars posticus; Pro., proscapulohumeralis; R. pro., rhomboideus profundus; R. sup., rhomboideus superficialis; T., triceps; Tpb., tensor patagii brevis; Tpl., tensor patagii longus.

to the tendon of *M. triceps;* the other branch runs distad the full length of the ulna, attaches to the bases of the secondaries and their major coverts, and fuses with the antibrachial fascia.

M. deltoideus major (fig. 1) arises from the acromion process of the scapula and from the well developed os humeroscapulare. There is a single insertion, which extends to about the junction of the middle and distal thirds of the humerus.

M. deltoideus minor is a thin strap of fleshy fibers about 10 mm long and 1 mm wide. It arises from the ventrolateral tip of the acromion process and inserts on the humerus at the junction of the head and deltoid crest.

M. subcoracoideus appears to arise by a single head from the posteroinferior surface of the coracoid. It inserts on the internal tuberosity of the humerus.

M. serratus posterior arises by fleshy slips from dorsal ribs 2, 3, and 4. The complex inserts by fleshy fibers on the apex of the scapula and by an aponeurosis anteriorly.

M. serratus anterior arises by a fleshy slip from the first dorsal rib. The band-like tendon passes upward between the two heads of *M. subscapularis* and inserts on the ventral edge of the scapula.

M. biceps brachii arises by a roughly L-shaped tendon from the coracoid and the humerus; its two tendons insert respectively on radius and ulna about 1 mm distal to their proximal articular surfaces. The belly is about 20 mm long and 6 mm in maximum width.

M. expansor secundariorum (fig. 2) has two tendons of origin. Beddard (1898:474) stated that this muscle is present in *Microhierax, Falco,* etc., but did not describe its structure. In *Polihiërax* a long tendon arises from the medial surface of the furcula near the junction of furcula, coracoid, and scapula. This tendon passes distad parallel to the humerus, and near the distal end of that bone gives way to a 10 mm-long, fleshy belly, which passes through the internal tricipital groove to insert on the basal ventral surface of several of the proximal secondaries. A second branch of this tendon runs posteroventrad toward the lateral side of the base of the coracoid, but could not be traced to a bony attachment. The extent of a connection between the main tendon and the fascia covering *M. dorsalis scapulae* could not be determined definitely in the one preserved specimen. The second major tendon arises from the entepicondyle of the humerus as in *Coua caerulea* (see Berger, 1953:59-60 and fig. 1).

M. pronator brevis (fig. 2) arises by a tendon proximal to the entepicondylar process of the humerus. Its insertion extends distad to within 15 mm of the distal end of the radius.

M. pronator longus (fig. 2) arises from the entepicondylar process of the humerus under cover of the humeral tendon of the expansor secundariorum. Its belly extends only about 1 mm beyond the insertion of the pronator brevis.

M. extensor pollicis longus has two separate heads. The ulnar head arises from a small area (about 4 mm long) on the proximal end of the ulna and the total length of its fleshy fibers is 13 mm. The second head is 16 mm long;

it arises from the second quarter of the radius. The two bellies give way to independent tendons, which fuse near the distal end of the forearm. The resulting single tendon inserts on the extensor process of metacarpal I.

M. abductor pollicis arises by a small tendon and by fleshy fibers from the tendon of insertion of the extensor metacarpi radialis and inserts on the basal half of the pollex. The two parts of this belly are not as distinct as in *Coua caerulea* (Berger, 1953:62-63).

M. flexor metacarpi brevis is a small round muscle whose belly is about 3 mm in length, but its diameter is less than .5 mm. It arises from the capsule of the dorsal ulnare-carpometacarpal joint and, about 5 mm distal to the base of the carpometacarpus, it inserts on the tendon of *M. extensor indicis longus*.

LEG MYOLOGY

The work of Hudson (1937, 1948) serves as an excellent basis for a discussion of the muscles of the pelvic appendage, so that the reader may assume that any muscle not discussed here is similar to that described for *Falco*.

M. gluteus medius et minimus is a small muscle (2.5 mm in length) which arises fleshy over a distance of 3 mm on the iliac crest dorsal to the acetabulum. It inserts by a thin tendon on the femur just proximal to the tendon of insertion of *M. ischiofemoralis*.

M. ambiens is a small, spindle-shaped muscle whose fleshy belly is about 15 mm long and only .5 mm wide. The belly extends distad a little more than half the length of the femur. Unlike the species of *Falco* studied by Hudson (1937:16 and 67; 1948: 104), in *Polihiërax* the tendon of the ambiens passes medial to the tendon of *M. biceps femoris*.

M. iliotibialis (fig. 3) arises by an aponeurosis from the anterior iliac crest and the anterior iliac process; there is no origin from the posterior iliac crest, and the belly does not cover any of the biceps femoris. The fleshy portion of this muscle is very small, being 7 mm wide and 13 mm long, though its

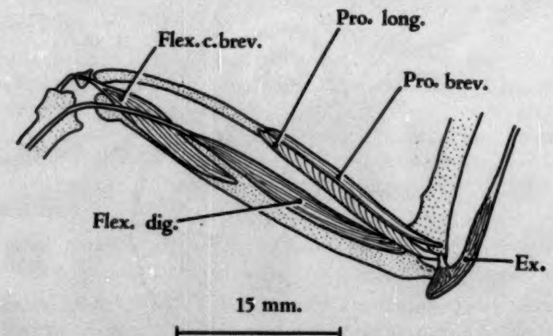

Fig. 2.—*Polihiërax semitorquatus*. Palmar view of right forearm to show relationships of certain muscles. Ex., expansor secundariorum; Flex. dig., flexor digitorum profundus; Flex. c. brev., flexor carpi ulnaris brevis; Pro. brev., pronator brevis; Pro. long., pronator longus.

anterior fibers are fused with *M. sartorius* and may extend farther distad than 13 mm. Distally its dense aponeurotic continuation fuses with the underlying *M. femorotibialis externus*.

M. femorotibialis internus arises from the medial surface of the femur, beginning 2 mm and 9 mm, respectively, inferior to the area of insertion of *M. iliacus* and the trochanter of the femur.

M. piriformis is represented only by *pars caudofemoralis* (fig. 3). This muscle arises by a 3 mm-long tendon from the base of the pygostyle. The belly, about 23 mm in length, and 5 mm in maximum width (near the insertion), inserts on the femur, beginning 7 mm inferior to the trochanter.

M. semimembranosus (fig. 3) is composed of two independent parts, though the areas of origin on the posteroventral edge of the ischium are adjacent. The two fleshy bellies pass distad toward the crus. The insertion of the posterior belly is typical for this muscle: by an aponeurosis (5 mm long and 1 mm wide) on the tibiotarsus, beginning about 4.5 mm inferior to the proximal end of that bone. The anterior belly arises anterior and somewhat dorsal to the posterior belly, and inserts by a flat tendon (3 mm long and 1 mm wide) deep to the medial femorotibial ligament on the posteromedial surface of the tibiotarsus, beginning 1.5 mm inferior to the proximal end of that bone. This is the usual area of attachment of the upper arm of the ligamentous raphe which separates *Mm. semitendinosus* and *accessory semitendinosus* when those muscles are present.

M. biceps femoris (fig. 3) arises by an aponeurosis from the entire posterior iliac crest. It inserts by a 1 mm-wide tendon on the fibula, beginning 7 mm inferior to the fibular head.

M. peroneus longus is a poorly developed muscle located in the distal half

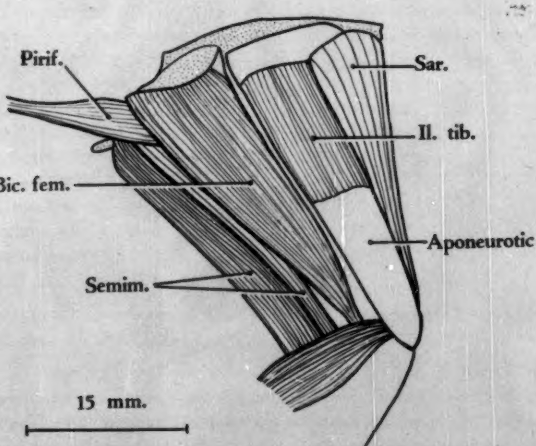

Fig. 3.—*Polihiërax semitorquatus*. Superficial muscles of the right thigh (lateral view). Bic. fem., biceps femoris; Il. tib., iliotibialis; Pirif., piriformis, pars caudofemoralis; Sar., sartorius; Semim., semimembranosus.

of the crus. It arises from the fibula and adjacent muscles as in *Falco* (Hudson, 1937:33-34). Its long tendon of insertion unites with the tendon of *M. flexor perforatus digiti III* about 6 mm inferior to the proximal end of the tarsometatarsus.

M. gastrocnemius consists of the usual three heads. *Pars externa* arises by a single head from the femur. *Pars interna* is weakly developed; it is a thin sheet of muscle (25 mm long), which does not extend around to the anterior surface of the crus. *Pars media* is relatively well developed, being half as long as pars interna.

M. plantaris is an unusually well developed muscle whose belly extends about three-fourths the distance down the crus. The tendon fans out distally and inserts on the entire proximal surface of the tibial cartilage. That structure, in fact, seems to be a continuation of the tendon of insertion of the plantaris. Only the tendon of *M. flexor digitorum longus* passes through a compartment in the tibial cartilage.

M. flexor digitorum longus has the typical V-shaped origin from the proximal end of the tibiotarus. Its belly (31 mm long) extends about three-fourths the distance down the bone. The tendon passes through a compartment in the tibial cartilage to the posterior surface of the tarsometatarsus, where it is united by a vinculum with the tendon of *M flexor hallucis longus;* both tendons are ossified. The tendon of the flexor digitorum longus trifurcates to supply digits II, III, and IV.

M. flexor hallucis longus is the most powerful muscle in the crus, and has two separate heads. The larger head arises by an ossified tendon from the intercondyloid region of the femur. The smaller head arises by semitendinous bands from the posterolateral surface of the femur proximal to the external condyle. At the distal end of the crus, the tendon expands into a thick mass (1.5 mm wide, 7 mm long, and .5 mm thick) which lies superficial to, and completely separate from, the tibial cartilage. At the distal end of the tarsometatarsus, the tendon bifurcates: the stronger tendon goes to the hallux, whereas the smaller tendon joins that tendon of the flexor digitorum longus which supplies digit II.

M. extensor hallucis longus arises by two separate heads from the proximal end of the tarsometatarsus. The smaller head (9 mm in length) arises medial to the tendon of *M. tibialis anticus;* its fleshy fibers give rise to a semitendinous sheet which fuses with the lateral head about midway the length of the tarsometatarsus. The larger head (17 mm long) arises lateral to the tendon of the tibialis anticus. The common tendon inserts on the base of the unguinal phalanx.

M. extensor proprius digiti III is rudimentary, being represented by a fleshy belly 4 mm long and .5 mm wide.

M. extensor brevis digiti IV is a poorly developed muscle whose fleshy belly is limited to the proximal half of the tarsometatarsus. At the distal end of that bone, the tendon passes through a bony canal to insert medially on the base of the proximal phalanx.

M. abductor digiti II also has a very small belly (about 4 mm long),

which arises entirely from metatarsal I and inserts on the dorsomedial corner of the base of the proximal phalanx, digit II.

M. flexor hallucis brevis arises fleshy from the tibial cartilage and from the greatly expanded medial hypotarsal ridge. Its belly extends a little more than half way down the tarsometatarsus. Its tendon does not ensheath the tendon of the flexor hallucis longus, but inserts on the middle of the plantar surface of the base of the proximal phalanx.

M. adductor digiti II is a triangular-shaped muscle, 4 mm long and 1.5 mm wide at its base. It arises on the posterolateral surface of the proximal end of the tarsometatarsus (the hypotarsus is a long ridge and not a rectangular process containing bony canals). The relatively wide (.5 mm), flat tendon inserts laterally on the base of the proximal phalanx, digit II.

M. abductor digiti IV is a poorly developed muscle, whose belly (8 mm long) is limited to less than the proximal third of the tarsometatarsus.

Discussion

The following wing muscles are absent: proscapulohumeralis brevis, abductor indicis brevis, abductor digiti II (probably ligamentous), and the biceps slip to the tendon of the tensor patagii longus. The flexor mass to digit III (*Mm. flexor digiti III and flexor brevis digiti III*) is poorly developed and seems to be part of *M. flexor metacarpi posterior. M. musculi cucullaris pars propatagialis* (of Gadow) does not insert on the tendon of the tensor patagii longus. *M. flexor metacarpi brevis* is present. *M. expansor secundariorum* is well developed. It has two main tendons of origin: a long tendon from the dorsomedial surface of the furculum and a short tendon from the entepicondyle of the humerus. *Mm. pronator longus et brevis* extend about the same distance distad on the radius. The structure of *M. extensor pollicis longus* differs from that which I have seen in other birds in that the radial and ulnar heads each give rise to independant tendons, though the insertion on the extensor process of metacarpal I is typical. I was unable to demonstrate a connection between the humerus and *M. scapulotriceps* ("*M. anconaeus*" of Beddard, 1889:81; 1898:474-475).

The muscle formula of the leg is ADAm. The following muscles are absent: piriformis, pars iliofemoralis (B), iliotrochantericus medius (C) [see Hudson, 1937:12-13, and 67; 1948:104 and 111], semitendinosus (X), accessorius semitendinosi (Y), adductor digiti IV, extensor brevis digiti III. *Mm. lumbricalis* and *extensor proprius digiti III* are rudimentary. *M. obturator internus* is triangular in shape; it does not arise from inside the pelvis as in *Fulica, Porzana, Coua caerulea,* etc. A vinculum connects the tendons of *Mm. Flexor digitorum longus* and *flexor hallucis longus,* and the latter muscle sends tendons both to the hallux and to digit II (Gadow's Type III). The tendons of *Mm. flexores perforati digiti III et IV* are perforated by the tendons to those digits from *M. flexor digitorum longus.* The tendon of *M. flexor perforatus digiti II* is not perforated by the two deep flexor tendons; nor is the tendon of *M. flexor perforans et perforatus digiti II* perforated by the tendon of *M. flexor digitorum longus.*

Polihiërax differs in leg myology from genera of the family Accipitridae in the same respects as *Falco* (Hudson, 1937:67; 1948:111). There are in addition certain differences between *Polihiërax* and *Falco*. In *Falco* the tendon of *M. ambiens* passes lateral to the tendon of *M. biceps femoris;* in *Polihiërax* the tendon passes medial to the biceps tendon. *M. semimembranosus* in *Falco* has two bellies which originate and insert together (Hudson, 1937:24); in *Polihiërax* the two bellies are separate throughout. In *Polihiërax* the tendon of origin of *M. flexor hallucis longus* is ossified; Hudson (1938:108) does not mention this for *Falco*. In *Polihiërax* the tendon of *M. flexor perforans et perforatus digiti II* is not perforated by the tendon of *M. flexor digitorum longus;* it apparently is perforated in *Falco* (see Hudson, *loc. cit*).

So little has been written on the wing myology of the Accipitridae and Falconidae that comparison with *Polihiërax* is not possible. It may be said, however, that *Polihiërax* differs in the following respects from other genera of the Falcones thus far studied: 1) the pattern of insertion of the tendon of the tensor patagii brevis is more complicated in *Polihiërax* (this character was considered important in classification by Garrod, Beddard, etc.); 2) *M. scapulotriceps* is not connected with the humerus; 3) *M. expansor secundariorum* arises by a tendon attached to the distal end of the humerus as well as by a tendon which arises from bones of the pectoral girdle; 4) part of *M. deltoideus major* arises from a well developed os humeroscapulare (scapula accessoria); Beddard (1898:479) mentions the presence of this bone in *Pandion*, thus implying its absence in other genera, but this probably is not true.

The true relationship between *Polihiërax* and other genera now included in the subfamily Polihieracinae cannot be known until the detailed anatomy of those forms has been investigated. Differences in leg myology noted above between *Polihiërax* and *Falco* seem too small to warrant placing these genera in separate subfamilies. However, it is necessary to know how much variation occurs in the appendicular myology within the family Falconidae before an intelligent statement on relationships can be made.

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Apparatus to Measure Forces Involved in the Landing and Taking Off of Birds

Harvey I. Fisher[1]
Department of Zoology, University of Illinois, Urbana

Study of the ways in which animals are adapted to live successfully in a particular situation has long been of interest to biologists. The early naturalists observed and theorized about some of the more obvious adaptations—the long legs in wading birds and the power of flight, for example. Explanation of the functioning of most of these gross adaptive mechanisms has been unsatisfactory.

Consider the wing of a bird. We can observe the movements it makes. By study of the structural components—the bones and muscles in a carcass—we note that shortening of a muscle or of a group of muscles may cause this or that movement. In a living bird, held stationary, electrodes inserted in various muscles may provide a means of correlating a movement and the contraction of a muscle or muscles. But these observations must be interpreted subjectively, and they are made under artificial and perhaps misleading conditions.

Investigation of such natural phenomena as the action of a muscle in a particular movement of the bird wing must be conducted in living, freely-flying birds. Further, there must be some quantitative measure of differences in function, if the results of these researches are to have inherent validity, to possess value for comparison with the findings of other workers, and to be of use in determining the degree of adaptation of a structure.

For several years I have tried to study the role of certain muscles in the wings of pigeons. Muscles have been removed, individually and in groups. Tendons have been cut, and muscles enervated. Slow-motion moving pictures taken before and after surgery were used to demonstrate loss of function.

It was difficult to assess the amount of change. The arc of the wing was "shorter," the tip of the wing was "not pulled quite so far forward," the alula "seemed to be used to a greater extent," and other similar subjective and indecisive observations were made. However, all the birds (68 individuals, involving 12 different surgical techniques) flew well in the large outdoor cages, maintained their body weights and, in general, were indistinguishable from control birds in the same cages. It was evident that a precise, quantitative method of ascertaining the change or loss of function had to be perfected.

Biological Basis of the Apparatus

In flight, it may be assumed that the greatest stresses on the structure of the wing and leg come at two different times. When a pigeon leaves the perch the legs and wings are strongly used to accelerate and to gain the desired momentum. In landing, deceleration is necessary. The wings are

[1] Present address: Southern Illinois University, Carbondale.

employed first, in a chronological sense, but the final stop is made by leg action.

The take-off involves more or less simultaneous muscular action in the legs and the wings. Using the laws of physics one can determine the force necessary to get a pigeon of a certain weight to moving at a certain speed. This force comes from leg and wing action. If we can determine the proportion of force provided by the legs, that part of the force coming from the wings may be calculated. For example, if total force were 100 units and 62 units of it came from the push of the legs, the component from the wings would be 38 units. A sufficient number of measurements of leg action in a single bird might set up a "norm" or average force contributed by the legs of that particular individual.

If there occurred any impairment of wing action, as the excision of a certain muscle might cause, there should be an increased component of force from the legs at the time of take-off or landing. The total force needed to accelerate or decelerate a definite mass (body weight of a pigeon) to a known speed remains constant. A number of measurements could be made to find an average increase in force from the legs. The probable significance of this increase could be calculated. If a truly significant increase were found, this increase in force could be called the contribution of force by the muscle that had been removed. Because of the synergistic action of muscles, this force might not be a true measure of the contraction of that particular muscle, but it would certainly be a valid quantitative index to a loss of function.

Similarly any weakening of leg action should result in an increased component of force from the wings when the bird takes to the air or when it lands.

In taking off and in landing, only the force of the legs can be measured. But, knowing total force and leg force, wing force can be determined. This is an indirect method of getting at wing action, but no method of any kind has ever been devised to measure the forces contributed by the wings.

Force exerted by the legs, during take-off or landing, is composed of three possible vectors—vertical, horizontal in the line of flight, and horizontal at right angles to the line of flight. We may call these downward forces, backward forces, and lateral forces, respectively. The problem then was to construct an apparatus to measure these three vectors of force.

Acknowledgments.—Professor Harold N. Hayward, Director of the University of Illinois Engineering Experiment Station Measurement Program, kindly consented to undertake the mechanical design and construction of the apparatus. Associated with him were Professor Howard C. Roberts and Instrument Technicians Hoyte L. Helms and William M. Norton. Mr. Helms and Mr. Norton were responsible for the definitive design and actual construction. To all these men go my sincere thanks for their interest and help during the two-year period of development; the machine now in use is the third "edition," the apparatus having twice been completely rebuilt and modified.

The University of Illinois Research Board provided funds for construction of the apparatus, and I am very appreciative of this aid.

Miss Doris Krull aided in the calibration of the instrument.

THE APPARATUS

Fig. 1 is a diagram of the machine[1] which is mounted on a piece of plywood

[1] Detailed specifications of bellows, tubing, etc., are available from the author.

(base) that is 15 by 26 inches and three-fourths inch thick. The landing platform (circumference is indicated by dotted line) is 15 inches in diameter, one-fourth inch thick, and covered by hardware cloth having a one-eighth inch mesh. The wire cloth gives a solid footing and prevents excessive slipping of the birds' feet.

The platform is supported by and fixed to three vertical bellows (A_1, A_2, A_3) whose lower ends are securely fastened to the base. Any downward pressure tends to compress these three bellows, causing the enclosed hydraulic fluid to move through the one-half inch copper tubes to a common chamber (M). In this chamber are ball cock valves which dampen the action. The only outlet from chamber M is tube X which leads to the horizontally placed bellows (A_4). Movement of the fluid in A_4 activates the lever-linkage with pen 1, causing it to move on paper wrapped around the revolving cylinder.

Bellows B_1 is horizontally placed in the axis of front to back movement of the platform. A rod in its left end attaches to the lower surface of the platform (near bellows A_1, but above this bellows). B_1 is also attached to the base. The right end of B_1 opens into tube Y which leads to bellows B_2 and to pen 2. It is not clear in the figure that B_1 has no connection to the chamber M. Each bellows-tube-pen system is necessarily a separate entity. Compression of B_1 by front or back movement of the platform thus causes pen 2 to record.

Bellows C_1 is supported by the base and attached to the platform, as indicated in the figure. The fluid in C_1 moves through tube Z to bellows C_2 and results in movement of pen 3. Since bellows C_1 is at right angles to B_1, the fluid in C_1 is moved by any lateral movement of the platform (top to bottom or bottom to top in the diagram).

The revolving metal cylinder is turned by a hand-wound clock mechanism governed by a butterfly release mechanism. A battery makes possible the use of a relay and a remote control wire. Already it is apparent that the clock should be replaced by a delicate electric motor to provide an even steadier speed of rotation. Preciseness is necessary here if one is to study the time factors involved.

The pens are simultaneously lifted from the cylinder by the pen lift (lower right in diagram).

Sensitivity and Calibration

A force of 50 grams, directed downward, backward, or to either side causes the appropriate pen to move. The record of a 50-gram downward force is constant, no matter where the force is exerted on the area of the platform. The same constancy is found with the other vectors.

However, the deflection of the pen is so slight and the width of the ink line so large, relatively, that consistent measurement of the deflection is difficult with forces as low as 50 grams. Accurate, consistent measurements are easily possible when the forces are of the magnitude of 100 grams. We have found that the downward force of a pigeon landing on the platform seldom is as little as 1200 grams. The possible error under these conditions may reach eight per cent, but the downward force may go as high as 4000

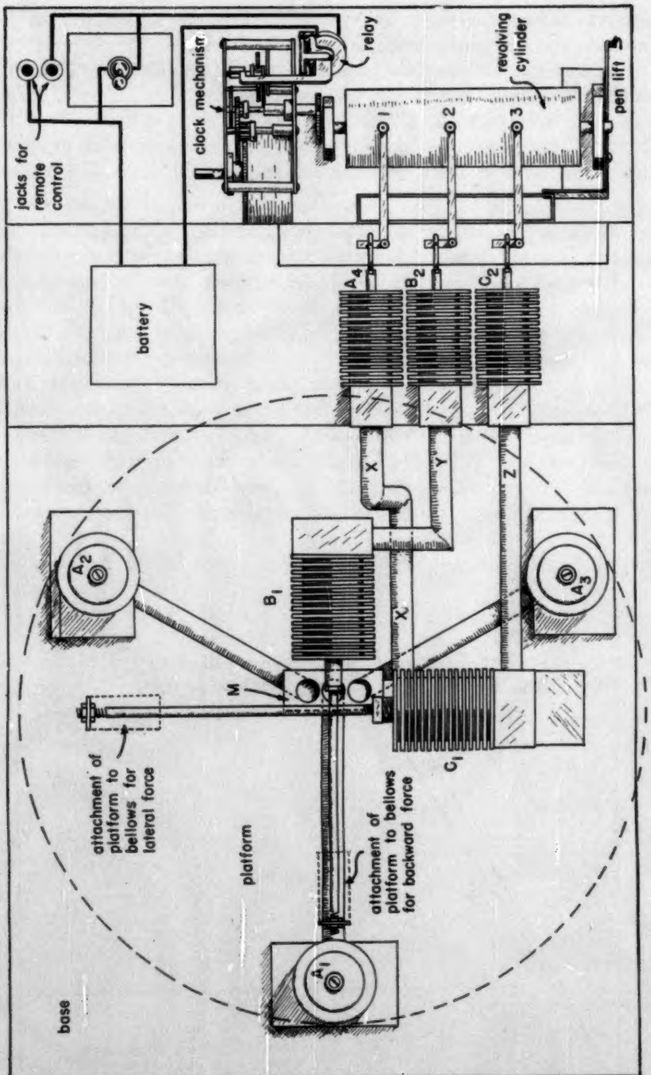

Fig. 1.—Top view of apparatus. Dashed circle represents landing platform. A1, A2, and A3 are hydraulic-filled bellows responding to downward vector of fcrce. M is a ball-cock valve to equalize forces recorded from A1, A2, or A3. B1 is bellows for front-back vector, and C1 is bellows for side to side forces. X, Y, and Z are tubes leading to bellows A4, B2, and C2, respectively. 1, 2, and 3 denote recording pens for down (1), front-back (2), and lateral (3) forces. These pens are activated by movements of fluid in bellows A4, B2, and C2.

grams and the backward force 2000 grams. As the force increases, the percentage error in the use of the machine naturally decreases.

Tests have shown that temperature has no demonstrable effect on the sensitivity, but all of our use of the machine has thus far been indoors at temperatures between 65 and 75° F.

In fig. 2 may be found the calibration data. Forces used in calibration were effected through gram balances. Points on the lines were determined

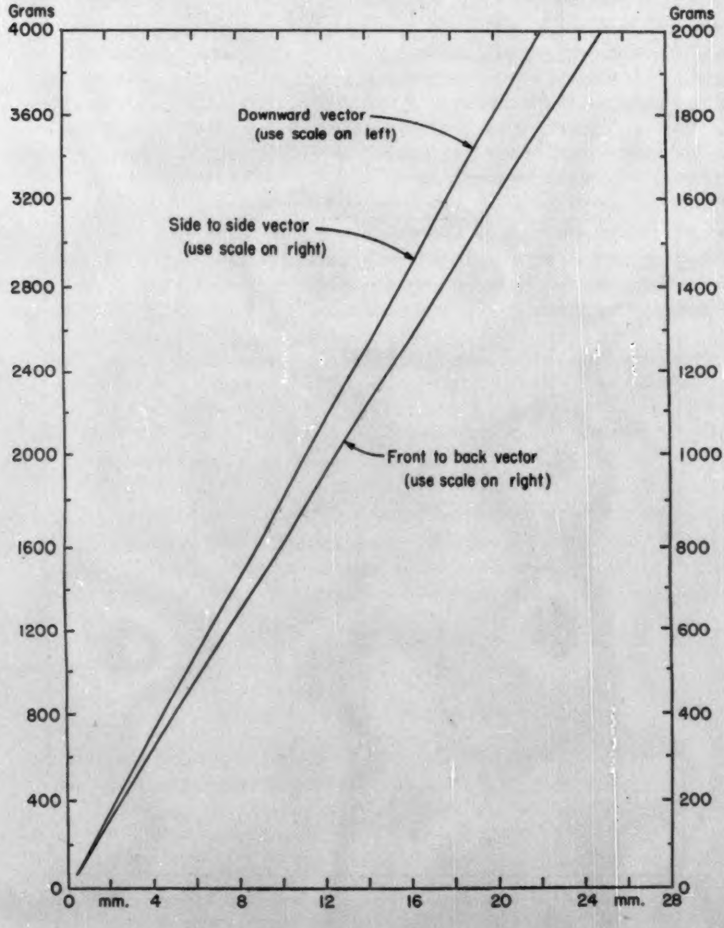

Fig. 2.—Calibration of the apparatus. Note that the deflections of the pens, as measured in millimeters, are linear in their relationship to the actual forces measured in grams. Further, the lines for the down and lateral forces are the same, except that the forces are different. (See the scales on the left and right sides.)

at intervals of 200 grams, and each point so represented is an average of 10 separate tests with the same force. The lines show that the instrument is virtually twice as sensitive for the lateral and backward vectors as it is for the downward force. The linear nature of the calibration "curves" gives further indication of the consistency of the machine.

USE OF THE MACHINE

For comparable results in successive trials on the same or on different birds, it is necessary for the bird to approach or to leave the platform in the same direction and at the same angle from the horizontal. In our laboratories the flight is directed by a muslin tube supported from above by a framework of heavy wire. The platform is placed in the lower half of one open end of the tube. The tube is supported in such a way that its long axis makes a known angle with the horizontal axis of the platform—20 degrees thus far in our work (fig. 3A). For domestic pigeons a tube or tunnel about 3 feet in diameter and 12 feet long works well. This diameter is excellent for this species because the bird, to have room to flap the wings, must fly almost exactly in the center of the tunnel. Thus the angle (from the horizontal) of its approach or departure from the platform is a constant. The 12-foot length provides sufficient distance for the bird to fly normally, balance itself, and land.

The long axis of the tunnel is a straight line continuing away from and

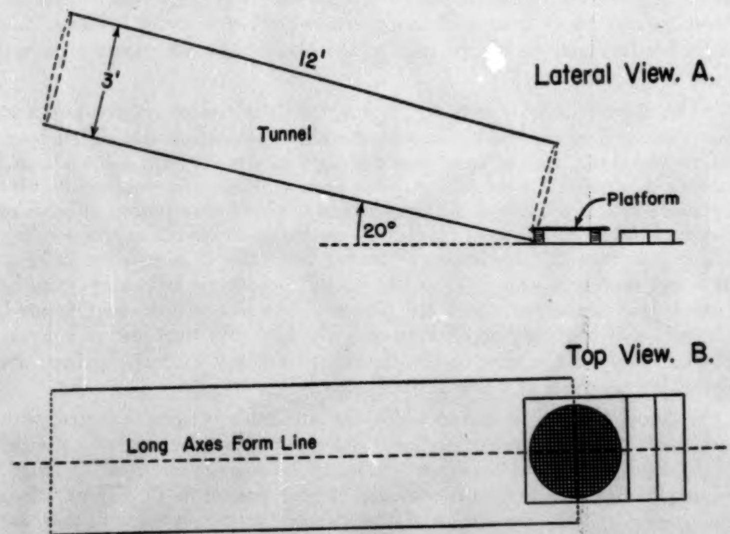

Fig. 3.—Diagram to show relationship between flight tunnel and landing platform. The angle of the tunnel may be varied as desired.

identical to the front to back axis of the machine. This arrangement is necessary to make certain that the bird approaches on this axis. Otherwise, the tracings of pens 2 and 3 (the back and lateral vectors) are not comparable from trial to trial (fig. 3B). In practice we discard any record which shows any significant force, other than that involved in the bird's balancing, in a lateral direction. Strong lateral forces usually indicate that the bird turned to right or left as it landed, and thus what is recorded as lateral force is really a part of the usual back vector of force.

For study of the forces in landing the bird is released at the upper end of the tunnel. It flies down the tunnel to land on the platform. Forces in take-off are recorded by quieting the bird on the platform; usually a hand covering the bird's eyes is sufficient. As soon as the bird is quiet the hand is removed and a slight motion by the other hand stimulates the bird to fly from the platform. All birds are handled in exactly the same way, even to using the same hand to pick up the bird.

Getting the birds to land and to take-off in proper fashion is not as easy as might be thought from the preceding paragraph. The bird must be flown, sometimes actually thrown, into the tunnel as many as 30 times before it begins to land on the platform. However, the muslin provides a poor perch; we purposely omitted the wire supports in the lower half of the circumference. The pigeon soon quits landing on the muslin. For some reason only one of our pigeons has ever flown all the way through the tunnel and out the open end above the landing platform. This happened only once. After the period of training one may expect about 80 percent success in getting usable records. Most failures result from off-balance, one-footed, or sidewise landings. At times one foot may be off the edge of the platform or the pigeon may land short of the platform.

The observer who releases the pigeon trips the remote control switch at the upper end of the tunnel to start the clock just before the pigeon lands on the platform. At the same time the flight to the platform and the actual landing is carefully watched. Another person keeps the landing in view through a hole in the side of the tunnel. Any pertinent observations of behavior that might affect the forces of landing are written on the record of that landing. The pigeon may skid on landing. It may hop once or twice after landing. Its wings may brush the sides of the tunnel, or one or both wings may be flapped just as the feet touch the platform. Only one foot may be used. The bird may obviously be off balance. The bird may turn just as it lands. The tail may hit the edge of the platform. Tracings of such landings are separated from those of the usual landings.

A "usual landing" is one in which the bird lands upright, balanced, with both feet more or less under its body, and the long axis of the body parallel to the long axis of the machine. Series of homogeneous "usual landings" frequently possess coefficients of variation ranging from 8 to 15. These values may seem high but, considering all the variable factors to control, they are not unduly high.

No training of the bird is necessary before measurement of forces during the take-off. The apparatus is set up in a room about 14 feet square. After

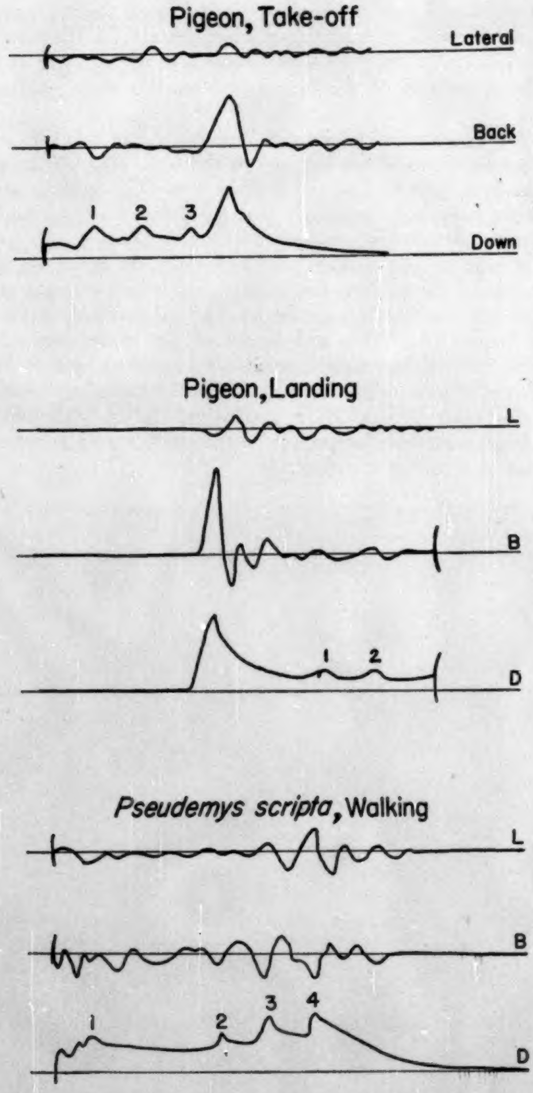

Fig. 4.—Tracings of characteristic recordings. Numbers 1 to 4 indicate peaks of force resulting from steps by the animal.

flying through the tunnel the bird is captured with an insect net. After 30 to 50 flights and 2 or 3 days of experience in the room, the net is unnecessary. Frequently after a record of a landing the bird remains on the platform while the mechanism is wound and the tracing paper is changed. Just as frequently it flies to the upper end of the tunnel and remains there until picked up in the hands.

In fig. 4 are some typical tracings of landings and of take-offs by pigeons. Here also may be observed the tracings of the walk of a *Pseudemys* turtle. Several turtles have been used in our experiments. The walking gaits of two species of ducks have been recorded. Records from the machine have been coordinated with slow-motion moving pictures. Thus it was possible to determine, for example, which foot produced which deflection on the record.

The principle of the machine can be used widely to provide a quantitative measure of various forces. Because the sensitivity depends upon the specifications of the bellows, the tubes and inertia of the entire system, from the platform to pens, it is theoretically possible to construct similar mechanisms to measure forces of vastly different magnitudes. Adaptations could be made to measure the force with which a grasshopper lands, with which a bird scratches, a frog or a rabbit jumps, or the kick-off force of a sprinter or the force of a foot of a runner in full stride.

A New Subspecies of Plethodon welleri, with Notes on Other Members of the Genus*

Gordon R. Thurow

Indiana University, Bloomington

The examination of 106 specimens of *Plethodon welleri,* from four of the five recorded localities for this species, convinces me that two distinct populations are represented. Walker (1934), Grobman (1944), and Snyder (1946) point out differences in specimens from various localities, but do not suggest subspecific distinction. These considerations and the results of my own studies make it seem worthwhile to summarize the present status of our knowledge concerning *welleri.*

Acknowledgments.—I wish to acknowledge the many courtesies extended to me by Clifford Pope, Robert Inger, and Hymen Marx of the Chicago Natural History Museum; Charles Bogert of the American Museum of Natural History; Dr. Doris Cochran of the U.S. National Museum; and Neil Richmond of the Carnegie Museum. The abbreviations CNHM, AMNH, USNM, and CM will be used in subsequent references.

PLATE I

Plethodon welleri ventromaculatum (paratype), CNHM 60105; *P. w. welleri,* CNHM 92994; and two specimens of *P. nettingi,* CNHM 92804-5, showing the approximate range of variation in ventral melanophore gapping in this latter species.

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* Contribution No. 566 from the Zoological Laboratories of Indiana University.

Plethodon welleri ventromaculatum, subsp. nov.

Plate I

Diagnosis.—Similar to typical *Plethodon welleri* but differing from topotypic material in that the majority of individuals have more conspicuous spotting of white pigment on the belly and lower flanks. Even when this spotting fades in preservatives, underlying gaps in the melanophore background are correspondingly developed so as to give a more heavily spotted appearance. The melanophore gaps are both larger and more numerous in the new form, and extend all the way along the lower flanks to the groin in most examples, whereas these gaps are smaller in most topotypes and rarely extend to the groin. Over 75% of preserved material is easily separable on this character.

Holotype.—AMNH 54448 (one of 11, study no. 790), adult male, collected on Mt. Rogers at 5500′ altitude, Grayson County, Virginia, on July 8, 1949, by C. M. Bogert and class.

Paratypes (24).—AMNH 5448 (10 specimens from same locality as holotype), CNHM 60102-5, 60522-5, same locality; USNM 124632-3, 133073-4, White Top Mt., Grayson Co., Va.; USNM 132323-4, 5.3 miles north of Carderview, Johnson Co., Tennessee, 2500′ altitude.

Range.—Specimens are recorded from Mt. Rogers and White Top Mountain in southwestern Virgina; from a spot 5.3 miles north of Carderview, Johnson Co., Tennessee, at 2500′ (between the southwestern extensions of the Holston and Iron Mountains); and Flat Top Mountain on the Tennessee-North Carolina border (south of Erwin, Tennessee). It is suspected that the range extends generally along the forested ridges of the Unakas between Mt. Rogers and Flat Top Mountain.

Material examined (*P. w. welleri*) (81).—Grandfather Mountain, near Linville, Avery County, North Carolina (all topotypes of the original description); CNHM 40452-3, 45921-38, 92990-93003, 93004 (paratype), 93005-28, 15988-9 (paratypes); AMNH 54034; USNM 84136-7 (paratypes), 118327 (?); CM 10994 (paratype), 6382 (25).

EXAMINATION OF THE STUDY MATERIAL

The characters which were examined and compared are indicated in the table below. The abbreviations *P.w.w.* and *P.w.v.* are used for the two subspecies. "Taxonomically significant" here means that over 75% of the material can be correctly assigned to one form or the other by examination of the character in question, or that the two populations can be distinguished by examination of individuals rather than only by derived statistical data.

PIGMENT

1. *Ventral melanophore gaps.*—*P.w.v.* has conspicuous gaps running along the ventrolateral area to the groin in most specimens, and present in varying degrees on the gular area and belly. *P.w.w.* has these gaps much reduced or absent, and none examined has the gaps along the whole length of the lower flank to the groin. *Taxonomically significant difference.*

2. *Belly darkness.*—Usually fairly dark in *P.w.v.*, although lighter than the dorsum, and some variation. There is more variation in *P.w.w.*, some approaching *P. metcalfi* in lightness. *Not a taxonomically significant difference, but P.w.w. may average lighter, statistically.* (None was examined as critically as for the preceding character, and few direct comparisons were made.)

3. *Suggestion of a dorsal band* (in preserved material).—An indication of a dorsal band is frequently present in *P.w.v.*, and is sometimes quite striking. Not only is there a thinning of the melanophore bed, but there appears to be a band of brownish pigment lying under the melanophores. These evidences were present less often in *P.w.w.*, and were not as strongly developed. *Not a taxonomically significant difference, but probably averaging stronger in P.w.v.* (All except CNHM 60522-5; USNM 124632-3, 133073-4, 84136-7, 118327; and CM 10994, 6382 were studied, and some of these were also examined.)

TEETH

4. *Number, arrangement, and shape of vomerine row; shape of parasphenoid patches; and distance between vomerines and parasphenoids.*—Both *P.w.w.* and *P.w.v.* generally agreed with the descriptions given by Walker (1931) and Bishop (1943). Counts of 4-6 were obtained, with 5 being the most common. The vomerine rows did not exceed the internal nares laterally, and curved inward and backward to be separated by roughly 2/3 to 2 diameters of the internal nares, depending on the varying development of both teeth rows and the internal nares. There is one raised parasphenoid area, containing two patches of teeth, which reconciles Bishop's and Walker's descriptions. The wide separation of the vomerines and parasphenoids is usually less than the length of a vomerine series, though of this magnitude, and near the 1½ to 2 nares diameters described by Walker. *No significant difference.* (The AMNH and CNHM material were first compared generally, with a few counts, and later detailed examinations were made of the AMNH 54448 series, AMNH 54034, and USNM 132324.)

TONGUE

5. *Size, shape, and surface pattern.*—In both *P.w.w.* and *P.w.v.* the tongue is broad and flat (this sometimes being modified by preservation), and almost fills the floor of the mouth, as described by Bishop. The tongue is thin-edged in this species, with plicae on the dorsal surface radiating from a point somewhat behind the center. *No significant difference.* (Same material as in 4.)

COSTAL GROOVES OR FOLDS

6. *Number and arrangement.*—In both *P.w.w.* and *P.w.v.* the specimens are as described for the species, most having 16 costal grooves or 15 folds. The range is from 14 folds plus an incomplete one, to 15 folds plus an incomplete one. *No significant difference.* (All the non-Grandfather specimens, all the USNM specimens, and several other AMNH and CNHM Grandfather specimens were counted.)

PROPORTIONS (see figs. 1, 2, and 3)

7. *The relation of tail length to head and body length.*—The tail grows at about 116% the rate of head and body growth in both *P.w.w.* and *P.w.v.*, and about the same sizes are reached. *No significant difference.* (Study nos. 788, 791, 794, 795, and 797 of AMNH 54448; AMNH 54034; CNHM 40452, 45921-4, 45928, 45931, 45933, 45936, 45938, 60103, 60524-5, 92991, 92993, 92997-93000, 93003, 93007, 93011-12, 93015, and 93021 were measured.)

8. *The relation of head width to head and body length.*—Growth of head width is about 12½% that of the rate of head and body growth, in both *P.w.w.* and *P.w.v.*, and about the same sizes are reached. *No significant difference.* (AMNH 54034 and 54448 (11); CNHM 40452, 45921-4, 45928, 45931, 45933, 45936-8, 60102-5, 60522-5, 92990-1, 92993, 92996-93001, 93003, 93007, 93011-12, 93014-15, and 93021 were measured.)

9. *The relation of head and neck length to head and body length.*—Growth of head and neck length is about 29% of the rate of head and body growth in both *P.w.w.* and *P.w.v.*, and about the same sizes are reached. *No significant difference.* (The same specimens were measured as in 8.)

SEXUAL DIMORPHISM

10. *Cloacal differences.*—In both *P.w.w.* and *P.w.v.* the males have cloacal gland papillae in the vent and sometimes the edges of the vent are produced posteriorly into two small flat lobes, as described by Walker and Bishop, and contrast with the simple slit shaped female cloaca. *No significant difference.* (Many specimens were examined casually. AMNH 54448 series were examined most carefully, as internal organs were revealed by previous dissection.)

11. *Mental gland.*—This is very poorly developed in both *P.w.w.* and *P.w.v.* males. *No significant difference.* (Examinations as in 10.)

12. *Ventral hedonic glands.*—The males of *P.w.w.* and *P.w.v.* have these glands weakly developed, and they are prominent only near the cloaca. *No significant difference.* (Examinations as in 10.)

The specimens available were examined for *any* possible differences, but no other characters showing significant differences were noted. Some of the observations given above add to the existing descriptions of the species, although they do not indicate subspecific difference.

All specimens examined were preserved, and this necessarily modified and limited the examinations. In particular, the principal character considered was the difference found in the number, size, and distribution of gaps in the melanophore ground pattern. In life, the most conspicuous character would be the difference in white spotting, since white pigment accompanies the sharp-edged ventral and ventro-lateral gaps. The relation between white pigment and the gaps was demonstrated by my examination of preserved and live *P. glutinosus* (Thurow, 1951). The same relation appears to be true in other species of *Plethodon* as well. Walker (1934) and Snyder (1946) probably refer to actual white pigment spotting, although Grobman (1944) refers to melanophore gaps, since he worked with preserved material.

Repeated comparisons were made concerning the melanophore gap character. Fifty-eight non-paratypic specimens from Grandfather Mt. (CNHM) were compared with a small series from White Top (CNHM 60102-5). In the Virginia specimens the gaps were obviously better developed, only two of the four specimens being overlapped by a single North Carolina specimen (CNHM 45925), and only one of these was nearly equalled in ventro-lateral gapping by the same specimen. The AMNH 54448 series (including the holotype of *P. w. ventromaculatum*) from Mt. Rogers was compared with the 58 Grandfather specimens and it was noted that about 11/15 of the Virginia specimens were distinct from the Grandfather material. The remaining specimens were distinct from about 90%. A second, more careful examination of all this material, plus another Grandfather specimen (AMNH 54034) gave similar results. None of the Grandfather Mt. specimens had the ventro-lateral gapping quite as heavily developed as any of the Virginia specimens. Fairly noticeable gapping occurs in only 20 of 59 of the former, and only on the anterior part of the flank. Only four North Carolina and three Virginia specimens are perhaps similar enough to be confusing. This represents less than 10% of the 74 specimens examined, and no more than 20% of either series. The same material was then randomized and rapidly sorted, as a test, and all but five were easily separable. It was decided that 80-90% of this material was separable, and that probably 80% of any sample could be correctly assigned by one familiar with the species.

Examination of material from other museums supports this hypothesis. Material in the USNM was easily separable. Virginia and Tennessee material (in USNM) appears to have heavier gapping than over 90% of all North Carolina material previously examined. Only one of 27 North Carolina specimens in CM might be confusing. Other material in the CNHM (930004, 15988-9, and 60522-5) is easily separable—only one Virginia specimens not being clearly distinguishable from about 5% of all the Grandfather material seen.

Snyder (1946) indicates that a specimen from Flat Top Mt. also had white ventral spotting.

Grobman (1944) states that the belly is darker in Virginia material than in typical *P. w. welleri.* He apparently compared only six Grandfather specimens with two from White Top. The different degree of gapping makes it difficult to compare belly darkness objectively. Examination convinces me that although most Grandfather material has about the same belly shade as *ventromaculatum,* a few individuals are much lighter. The greater extremes of lightness and greater range of variation in the Grandfather material *may* be due to a larger sample. I believe that the comparison of large live series will establish a slightly lighter average belly color in *P. w. welleri.*

In regard to the dorsal band, a deep lying band of brownish pigment (probably reddish in life, but hidden by melanophores) appears to be present in some specimens from all four localities. This is mentioned only in Walker's description (1931). The deeper lying brown pigment is definitely *not* synonymous with the superficial gold pigment. Indications of a band are probably much more apparent in preserved specimens, where the overlying gold pigment has disappeared and the underlying tissues have become opaque, reflecting light back through the thinned melanophore area. The band has wavy margins rather than pointed lobes as in many *dorsalis,* and commonly splits in to a "Y" as it passes onto the head. The shape is somewhat reminiscent of the irregular stripe of *yonahlossee* or *ouachitae.* After seeing changed red, white, and black pigment in thousands of *Plethodon,* mostly *cinereus, dorsalis,* and *glutinosus,* this hidden band seems quite certain to me, particularly in such specimens as CNHM 60105 and 60522-5, and USNM 132323-4.

Live *ventromaculatum* might possibly possess subspecific differences such as heavier dorsal gold markings, or dorsal markings of a slightly different color. However, if such differences exist, they were not striking enough to elicit comment from Walker (1934) or Snyder (1946).

The costal groove situation is exactly as reported by Walker (1931), where one groove is counted in the axilla and the groin, but it might be useful to mention the variation of the posterior grooves. Sometimes, the last groove is slanted forward to intersect the next, giving a forked groove, or "15½." Sometimes, there is still space for a full costal groove behind this, giving "15½ plus 1" which is equivalent to "16." Sometimes, the last fold is thinner at the bottom, giving the "16 minus." More frequently, the variations are toward an incomplete 15th fold than towards any extra. Only one "16½" and one "17 minus" were encountered.

Data on body proportions are presented in figs. 1-3. The straight line regressions indicate a constant growth relation, the relative rates of which can be simply calculated by measuring the coordinates to find b of $Y = a + bX$. The initial suspicion of a stouter, less elongate *ventromaculatum* appears to be false, but measurements of still other proportions in live series may show differences. Well preserved specimens, with a minimum amount of body distortion or tail mutilation, were chosen for measurement. The measurements were taken repeatedly to 0.1 mm with a dial calipers, and rounded off to 1 mm for the longer measurements. Head width was measured to the angle of the jaws, across the posterior part of the skull. Snout-to-forelimb length was taken along the ventral surface. Body length was taken along the ventrum, from the snout to a point between the posterior margins of the hind limbs. (This seems to be more satisfactory than measuring to either end of the cloacal slit, since this

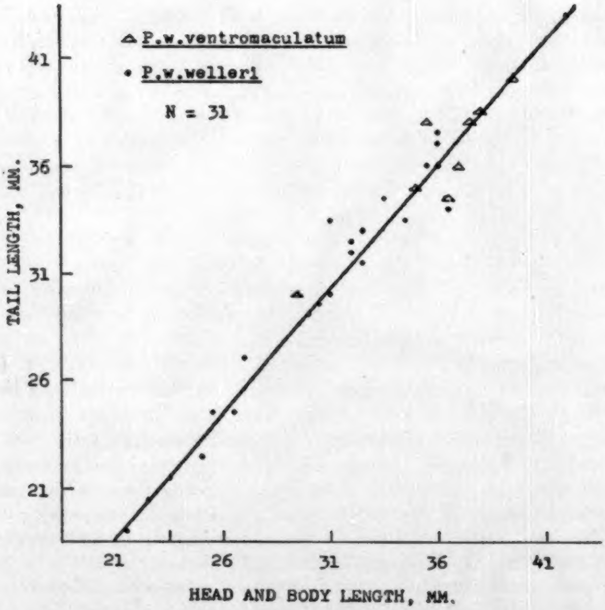

Fig. 1.—The relation of tail growth to head and body growth in *P. welleri.*

may vary in position and size with relation to the pelvis.) Tail length was taken from the same point.

Male cloacal gland papillae or villosities are the most reliable external secondary sex character, as described by Pope and Pope (1949) and figured by Noble (1931, fig. 104).

The mental gland is so poorly developed as to be almost absent. No doubt this varies seasonally, but no *welleri* were seen with mental glands comparable to *P. cinereus, dorsalis,* or *glutinosus.* In eleven specimens from Mt. Rogers (AMNH 54448) there was only a slightly lighter color of the skin at the mentum and along the jaw rami. There is some suggestion that this lightening is caused by a diffusable substance originating in the mental gland tissue (Thurow, 1951). These specimens were collected July 8th. Slightly better development was noted in a Grandfather specimen (AMNH 54034) taken September 2nd, which hints at fall breeding activity.

Hedonic glands are described by Noble (1929), and ventral hedonic glands in *Plethodon* are discussed by Thurow (1951). Some males of *welleri* apparently have hedonic glands just above the posterior angle of the postorbital groove, a position in which they have apparently not been observed in other *Plethodon,* although they have been reported as occurring there in other plethodontids and salamandrids (Noble, 1931).

The slightly more pointed male jaw tip and more swollen nasolabial groove areas with more noticeable tubercles, mentioned by Bishop (1943) and Walker

(1931), are certainly not strikingly obvious in males of the *welleri* material examined; but are probably present. The very slight sexual dimorphism in proportions that may exist would require statistical analysis of rather large samples for demonstration.

In general sexual dimorphism in *P. welleri* appears to be poorly developed compared to the condition in such forms as *Eurycea bislineata,* or even *P. glutinosus.*

DISCUSSION

THE VALIDITY OF VENTROMACULATUM AS A SUBSPECIES

The above description and discussion make it clear that the only easily demonstrable distinction between the Grandfather and non-Grandfather populations of *welleri* is in small differences in pigment. The magnitude of this difference is not much greater than that occurring within the geographically limited *P. nettingi,* as is roughly shown in Pl. I. More widely distributed forms such as *P. richmondi* and *P. cinereus* vary widely in this character according to my observations.

I think, however, it is widely agreed that subspecies are not everywhere equivalent as to degree of visible morphological differences. This is not to argue that any two noticeably different populations deserve names, but rather that other criteria besides degree of morphological difference should be used. At the present time the differences between the Grandfather and non-Grandfather populations appear to be consistent and diagnostic, even though they are small. For this reason, I think it useful to give them names and regard them as slightly differentiated insular races. If further collecting reveals a large number of exceptions, or reveals that the populations are merely ends of a cline, then the second name can of course be discarded.

THE DISTRIBUTION OF P. W. VENTROMACULATUM AND P. W. WELLERI

If it is accepted that the four populations from localities other than Grandfather Mountain, represent a single subspecies, then one would expect to find

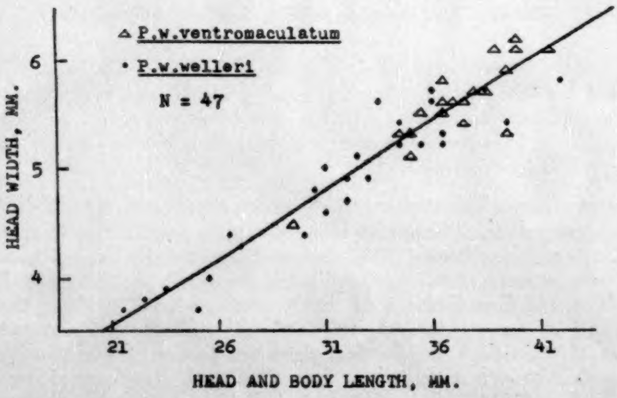

Fig. 2.—The relation of head width growth to head and body growth in *P. welleri.*

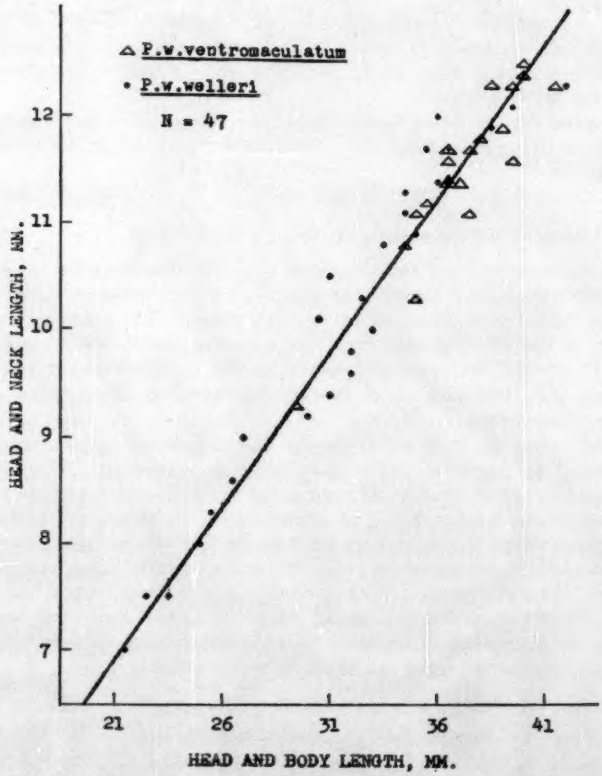

Fig. 3.—The relation of head and neck growth to head and body growth in *P. welleri.*

greater continuity of the populations among these areas than between any of them and the Grandfather Mountain locality. If all *welleri* populations are completely isolated mountain top relicts, and have been so for any length of geological time, even greater taxonomic differences might be expected to occur between the various locations.

Certain evidence indicates that the *P. welleri* populations are not all isolated mountain top relicts. The species may represent a parallel case to that of *P. yonahlossee,* which as Pope (1950) points out is not such a high altitude form nor so rare as some may think. Although the specimens from Mt. Rogers, White Top, and Grandfather are from elevations of 5,000′ or above, the specimen from Flat Top was taken below 4900′, and the Johnson Co. material was taken at 2500′ in the valley between the lower prongs of Holston and Iron mountains. Although most authors list *welleri* as an inhabitant of the spruce forest, Walker (1934) admits that a few individuals were taken further down in the upper hardwood level, and the crest of Flat Top is covered by beech-

birch forest. It is possible that the species has not been taken more frequently at lower altitudes simply because no intensive search has been made.

The dates which I have been able to obtain for collections of *welleri* are distributed as follows: April (2), May (2), June (1), July (3), August (11), and September (4—all in the first nine days). I believe these figures are due to more summer collecting, rather than greater summer abundance. Even in the moist southern Appalachians these are the warmer months of the year and have the highest evaporation rates. The low altitude records from Holston Mt. and Flat Top Mt. are both for May. It is not inconsistent with what we know about terrestrial plethodontids to think that it is probable that *welleri* is quite secretive, remaining well beneath the surface of the ground during the warmer months, particularly at the lower altitudes. This does not mean that the form is absent, except from the more superficial surface retreats. The converse is intimated by the fact that Pope (1950) found the species under bare rocks imbedded in the grass in the full July sun, at 5880′ on Grandfather.

It, thus, seems possible that *welleri* will be found in a number of other localities, and if these populations connect the two forms morphologically over a large enough area, the subspecific entity erected here would be unjustified.

This, however, does not seem to be the situation. What then separates the populations of the four known *P. welleri ventromaculatum* localities from that of the Grandfather Mountain area and connects them with one another?

Consideration of distance and altitude give mixed results. White Top and Mt. Rogers are clearly closely adjacent peaks on one mountain mass, as is shown by the 4,000 foot contour on the sectional aeronautical chart, and their populations are almost certainly confluent at the present time. The Holston Mountain locality is roughly equidistant from White Top and Grandfather, being about 30 airline miles away from either. Flat Top Mountain is roughly the same distance from both Grandfather and the Holston Mountain locality. Grandfather is about 40 miles from White Top. These considerations do not greatly injure the idea that the Virginia and Holston Mountain populations are taxonomically identical and separate from the Grandfather population, but they do cast some doubt on the alliance of the Flat Top specimen (which was not seen).

Considering altitude the situation is even worse. The 3,000 foot contour places the Grandfather and Virginia locations on the same mountain mass and the Flat Top and Holston localities on two separate outliers.

Physiographically, however, the known localities for *P. w. ventromaculatum* all fall into a line running southwest to northeast roughly paralleling the Tennessee-North Carolina border and flanking the mountain mass just southeast of it. This line falls within an area of mountain ridges, similarly oriented and also flanking the main mountain mass. A rough connecting pathway can be detected running from White Top through the Iron Mountain ridge (which is connected to the Holston Mountain Range), the Stone Mountain Ridge, and the Unaka Mountains to Flat Top. About three or four narrow cross-valleys, under 2,000′ elevation, interrupt this path, and continuous populations certainly do not exist along its entire length at present. However, as recently as 2,000 to 600 years ago, before the present amelioration of the so-called "little ice age," the climate was much cooler than the present warming cycle; and

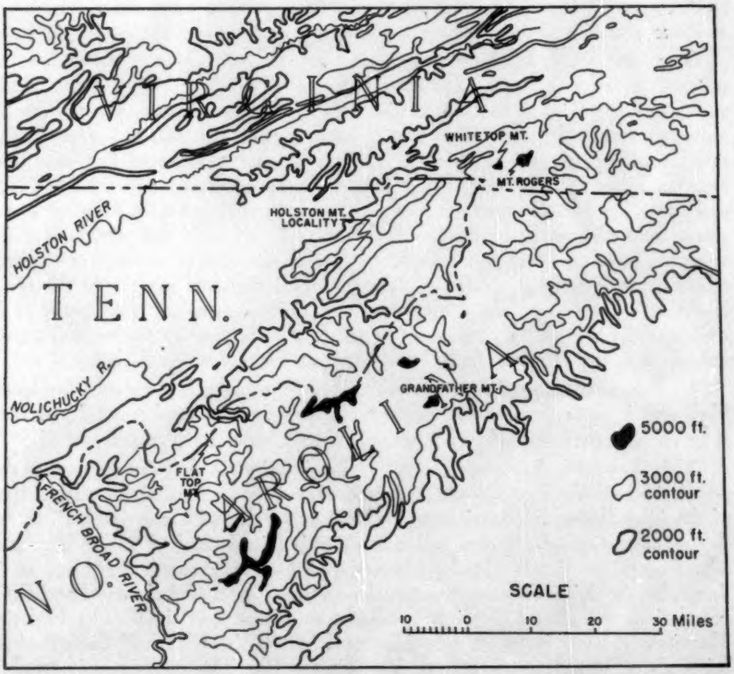

Fig. 4.—Contour map of the southern Appalachian Highlands, showing the five localities from which *P. welleri* has been collected. Modified from U.S. Coast and Geodetic Survey Regional Aeronautical Chart 14M (covering sections R-8 and S-8, Charlotte and Winston-Salem), 1944. Drawing by John Peace.

biotic altitudinal zones were no doubt lower. Considering this, the present 2500′ record for *welleri,* and the fact that there was no deforestation, the 2,000′ valleys cease to be formidable barriers. A similar pathway can be traced from White Top to Flat Top through the main mountain mass, of course, but such a path through the jumble of peaks and criss-cross ridges would not have the physiographic continuity of these parallel ridges. Grandfather Mountain is known to be a rather isolated peak physiographically. The situation is shown more convincingly by the Roan Mountain topographic sheet (U.S.G.S.) than in fig. 4.

The present taxonomic alignment of these populations is even more strongly supported by the geology of the region. The parallel flanking ridges have a similar structural basis in that upturned, folded, and faulted Cambrian strata abut against the precambrian crystalline rock of the main mountain mass. Fenneman (1938) comments on this situation. (See also Kieth (1903), Nelson (1928), Rodgers (1952), and a simplified geologic map of N.C., N.C. Dept. of Conservation and Development, 1937.)

Certain strong formations such as the Unicoi and Erwin formations form ridges running from Flat Top Mountains to merge with the Blue Ridge proper at Mt. Rogers. Kieth's (1903) description of the weathering of these formations indicates that not only do they form high ground, but that the slopes are rockier than those covered by weathering products of more easily decomposed formations. The point is that weathering of metamorphosed sedimentary rocks, as in these neighboring mountain ranges or "Unakas," is more likely to produce boulder fields, talus slopes, and other mantles of *coarse* weathering products thus offering deep crevices for salamander retreats. Such coarse waste is rare in the Blue Ridge itself as is indicated by the remarks of Fenneman (1938) and Kieth (1903) on the weathering of crystalline rock. Such differences apparently do not have any great effect on plethodons such as *cinereus, glutinosus,* and the *jordani* group. They are, however, important to some species. Work in progress on *dorsalis* indicates that coarse rock weathering products in the underlying substratum are very important. The occurrence of the Flat Top specimen in a rock field heightens the suspicion that this factor may be important to *welleri* also.

The most striking phenomenon is that the isolated Grandfather population occurs in an isolated area of Cambrian rocks, mostly the same Unicoi Formation that is important in the ridges to the west, but separated from it by Kieth's Cranberry Granite (1903). His description of the easy decay of this rock (although it has a large content of insoluble materials); of the resultant smooth, rounded knobs and slopes; and of a large part of the area being covered by tillable light loams of fair depth, indicates that this crystalline rock in particular might form an unfavorable substratal habitat. An intermediate area of Beech Granite is not quite so unfavorable, and may have formed a partial bridge to the Unakas under some more favorable climate. The local erosional history would tend to affect this. The broad band of Cranberry Granite separating the Grandfather Cambrian deposits from the Unakas continues well past Mt. Rogers into Virginia. Another interesting fact is that although the White Top-Rogers mountain mass might be expected to be pre-Cambrian crystalline material by virtue of its position, it actually is an isolated patch of metavolcanic material which originally was extrusive, and has weathering properties more like the strip of metamorphic Unicoi Formation with which it is contiguous than with the Cranberry Granite (here called Grayson Granite Gneiss) bordering its other sides.

The geologic pattern outlined above seems to fit perfectly with the taxonomic alignment present here, if later field work shows it to be meaningful. If it is later shown that Grandfather Mountain and the Virginia mountains are partly surrounded by geologically unfavorable formations, this would be a further partial explanation of why *welleri* seems to be so limited to the upper part of these peaks.

Some localities which should be carefully searched for *welleri* according to the preceding ideas are Iron Mountain, Holston Mountain, Stone Mountain, Unaka Mountain, Roan Mountain, and Beech Mountain, although careful search of the peaks of the main mountain mass between Grandfather and Mt. Rogers should also be undertaken as a check.

THE PHYLOGENETIC SIGNIFICANCE OF PLETHODON WELLERI VENTROMACULATUM, AND THE RELATION OF WELLERI TO OTHER PLETHODON

The primitive characters of *Plethodon* listed by Dunn (1926) are 1) few costal grooves, 2) long vomerine series, and 3) the presence of dorsal light markings. Primitive characters listed by Hairston and Pope (1948) are 1) large size, 2) long vomerine series, 3) lack of sexual dimorphism, and 4) a colored dorsal pattern. The later list not only differs in the addition of sexual characters, but "few costal grooves" are not necessarily directly correlated with "large size" in an unambiguous manner if size is measured by head and body length or by total length. A salamander may be generally large or may merely be elongated, as in *Batrachoseps*. Although the "Large Plethodons" (Grobman, 1944) have fewer costal grooves than the "Small Plethodons" (Grobman, 1944), *P. welleri* which has fewer costal grooves than *P. richmondi* is definitely smaller, particularly in total length due to the greater elongation of the tail (Green, 1938, Grobman, 1949). According to size, *welleri* would be the least primitive member of the "Welleri Group" (Grobman, 1944), but on the basis of the costal groove count it would be the most primitive.

I believe that the fact that *welleri* has the lowest costal groove count of any "Small Plethodon," and is also proportionally most like the "Large Plethodons," indicates that it is the most primitive rather than the most specialized in these respects. This is not contradicted by the low degree of sexual dimorphism (which is definitely less than that of *nettingi, huldae,* richmondi, dorsalis,* or *cinereus,* according to my observations), nor by the length of the vomerine series. Walker's description of *welleri* gives the vomerine series as 5-7, which is the number given for other "Small Plethodons" by Bishop (1943), and is common in all of them. I have found counts of 4-6 for *welleri* and 3-7 for *cinereus*. The partly-concealed dorsal band of *welleri* and the extensive golden patches represent a more primitive pattern than that of *nettingi, richmondi,* or the black phase of *cinereus,* but not of typical *dorsalis* and the red-backed phase of *cinereus*. The shape of the band is more primitive than in red-backed *cinereus* according to Dunn (1926), and its presence indicates that *welleri* is not necessarily so sharply separated from *dorsalis* and *cinereus* as Grobman's groupings (1944) would suggest.

Grobman (1944) distinguishes the "Cinereus Group" and the "Welleri Group" largely on the criteria that the former have a dorsal band and no dorsal "greenish golden to brassy" flecks, and that the latter lack a band and do have flecks. Careful examinations have shown that most live *dorsalis* and *cinereus* of both phases *do* have brassy flecks, and that some preserved *welleri* show more evidence of a band than many melanistic *dorsalis*. *P. richmondi* also has been observed to sometimes show evidence of a melanophore-obscured band (Bishop, 1943). The "Cinereus Group" and the "Welleri Group" do not appear to be justified.

The above considerations also suggest an alternative to the phylogenetic relationship suggested by Green (1938). His hypothesis that *welleri* and

* Found to be a synonym of *cinereus* by the work of two other authors and myself—some or all of this work to be published elsewhere.

nettingi are localized, dwarf, montane derivatives of some pre-*richmondi* stock implies that *richmondi* is more primitive. Grobman (1944, 1949) concurs with the hypothesis. Studies now in progress suggest that *richmondi* is more closely allied to *cinereus* than to *welleri*.

The logical extrapolation of the hypothesis presented here makes it seem likely that *welleri* is a dwarf derivative of some form more nearly like *yonahlossee* than *richmondi*, although not closely related to either.

It is perhaps futile to speculate as to which *welleri* subspecies is more primitive. If there is a larger Unaka Mountains population and a small Grandfather population, which are parts of a once larger range, then it seems more likely that the smaller population would have differentiated farther from the original state simply through genetic drift, although this is not necessary. If the primitiveness postulated for *P. yonahlossee* by Pope (1950) is accepted, it will be seen that the variable state of belly spotting represented by that form (Pope 1950, fig. 4) has given rise to an increased amount of mottling, as in *cinereus*, and to a decreased amount, as in *metcalfi*. *P. welleri ventromaculatum* is apparently nearer the median condition shown in Pope's figure and *P. welleri* is apparently similar to the less-spotted example or even more unspotted. This would suggest that *P. welleri* is the more divergent subspecies, as would also the possible poorer development of its cryptic dorsal band. This would be in accord with the probability of genetic drift.

SUMMARY

A study of museum specimens of *Plethodon welleri* was made in which 106 specimens were examined. A new subspecies is recognized and described. This form, *P. w. ventromaculatum*, differs mainly in having a greater degree of spotting on the venter. It has been found on White Top Mountain and Mt. Rogers in southwestern Virginia, between the south prongs of the Holston and Iron Mountain ranges in northeastern Tennessee, and on Flat Top Mountain on the Tennessee-North Carolina border. Photographs and a distribution map are presented.

Specimens were studied with regard to pigment, mouth characters, costal grooves, proportions, and various skin glands and sexual characters. Some information about the species is added from these observations. General comments on pigmentation and on secondary sexual characters in the genus *Plethodon* are included.

The validity of and criteria for subspecific differentiation are discussed. Ecological, physiographical, and geological factors concerning the distribution of the two subspecies are also considered, and their bearing on the assumption that the two actually represent insular races occupying respectively: (1) the metamorphic Unaka Mountains along the western flank of the Blue Ridge, and (2) Grandfather Mountain which is well within the Pre-Cambrian crystalline part of the Blue Ridge Province but is also made up largely of Cambrian metamorphosed sedimentary rock. It is pointed out that the ideas presented herein on the taxonomy and distribution of the species may be changed by further collecting, and several test areas are suggested.

The relationship of *welleri* to other species of "Small Plethodon" are dis-

cussed, and reasons given for the belief that the species is primitive rather than advanced. It is thought more likely that *welleri* arose from some form unlike any other "Small Plethodon" except *welleri* itself, or possibly *dorsalis*, rather than from a *richmondi*-like form, as has been proposed. The views expressed differ from the phylogenetic schemes of both Grobman (1944) and Green (1938). The possible phylogenetic relationships of the two subspecies are briefly considered, in relation to their population sizes.

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The Gnathosoma of Megalolaelaps ornata (Acarina—Mesostigmata—Gamasides)

Flora Gorirossi Bourdeau[1]
North Carolina State College, Raleigh

Megalolaelaps ornata is the second gamasid mite to be studied in the present series of investigations on the feeding apparatus of the mesostigmatid mites. *M. ornata* was originally described by Keegan in 1946. He found three specimens, two female and one male, on the window of a hospital ward in Camp Crowder, Missouri. The specimens used for the present study were recovered from *Pinotus carolinensis,* the common dung beetle. A single pair with one or two immature forms were usually found on a single beetle.

The methods used for study were the same as given in a recent paper on *Megisthanus floridanus* (Gorirossi and Wharton, 1953). The lateral view (Pl. II) is a composite drawing taken from serial sections cut at 10 microns.

Acknowledgments.—The author wishes to thank Dr. Wharton for his advice and criticism. Special thanks are extended to Mrs. Hansens for her artistic collaboration in presenting the three dimensional drawing of the feeding apparatus of the gnathosomal parts (Pl. II).

Gnathosoma.—The gnathosoma of *M. ornata* projects from the anteroventral surface of the idiosoma, anterior to coxa I. The gnathosoma of the male can be readily distinguished from that of the female. Other than the characteristic mesostigmatid features on the gnathosoma the female is devoid of ornamentation; in the male a pair of prominent protuberances project from the ventral surface of the hypostomal region just posterior to the distal hypostomal seta. Another feature of the male which is lacking in the female is that the corniculi are provided with teeth on their medioventral surface; those of the female are smooth. As in *Pergamasus vargasi* (Gorirossi, 1955c) the chelicerae offer the most striking differences between the sexes.

Gnathosomal base.—(Pl. I A, D; II) The ventral surface of the gnathosomal base (c) has two ridges which extend on either side of the deutosternum —one above and one below the level of the gnathosomal setae. They arise from the same level as the first and third row of deutosternal teeth.

Deutosternum.—The walls of the deutosternum (u) distinctly delineate it from the ventrolateral walls of the gnathosomal base. It contains seven rows of anteriorly directed teeth. These teeth never reach the walls of the deutosternum but are restricted to its central portion. The teeth are more numerous in the female than in the male. The deutosternum measures 328 microns in the male and 310 microns in the female.

Gnathosomal setae.—The gnathosomal setae (w) in both sexes arise at a level between the second and third row of deutosternal teeth. They are nude.

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In most specimens examined the gnathosomal setae of the male are longer (160 microns) than those of the female (147 microns).

Horizontal shelf.—(Pl. I E, I-K; II) The horizontal shelf with its components—the epistome (i), tentorium (m), subcheliceral plate (d) and posterior epistomal process (i′)—is comparable to that described for *P. vargasi* and will not be described here. The bars of the subcheliceral plate are approximately 269 microns long.

Cheliceral sheaths.—(Pl. I J-L; II) The cheliceral sheaths, their insertion and origin, and relation to the horizontal plate is the same as described for *P. vargasi.*

Pharynx.—(Pl. I J, K; II) The triradiate pharynx and the insertion of its muscles are the same as described for *Uropoda agitans* (Gorirossi, 1955a).

Tectum.—(Pl. I G; II) The tectum of the male and female are mucro in shape. From its edge extends a dentate, narrow, lightly sclerotized membrane. The tectum of the male measures 657 microns long and 437 microns wide; that of the female measures 437 microns long and 312 microns wide.

Epipharynx.—(Pl. I A, E, L, M; II) The epipharynx (j) is approximately 458 microns long and can be readily seen from a ventral view between the hypopharyngeal processes. It is a long, slender structure covered from tip to base with small, anteriorly directed spines. The epipharyngeal muscles (n) which insert along its base originate from the proximal edges of the bars of the subcheliceral plate (d) and the epistomal process (i′).

Labrum.—(Pl. I E, L; II) The labrum (h) of *M. ornata* is a long, tapering structure which measures about 324 microns long. It is very narrow and flexible anteriorly but posteriorly is as wide as the anterior surface of the epistome from which it extends. At the point where it widens the sides of the labrum are deeply fringed.

Hypopharynx.—(Pl. I E, I, L, M; II) The hypopharyngeal walls (q) are lined with a series of anteriorly projecting spines and ridges which radiate medially from the lateral edges. From the dorsal surface of the hypopharynx project the small, slender hypopharyngeal teeth (g).

Hypopharyngeal processes.—(Pl. I A, D, E, I; II) The hypopharyngeal processes of *M. ornata* are more difficult to define than in some species. From the study of the hypopharyngeal region made here it appears that the processes are divided into two portions which arise from a common base. One is ventral and the other dorsal. The ventral portion consists of a pair of long, slender lobes which project from the protosternal region. It is between these lobes that the epipharynx can be seen from a ventral view of the gnathosoma. The dorsal constituents of the processes arise from these ventral lobes about midway along its length. They are shorter and not as round as the ventral portions (I). When further study is made on the embryology of these forms it may be found that the ventral portions of the hypopharyngeal processes are actually the hypostomal processes. They have not been recognized as such here because they do not arise from the walls of the hypostome.

Hypostome.—(Pl. I A, D) The hypostomal region (k) supports anteriorly the corniculi and posteriorly is continuous with the gnathosomal base. In the female it is devoid of ornamentation except for the hypostomal setae.

In the male, however, in addition to the hypostomal setae, an egg-shaped protuberance projects ventrally from the hypostomal wall just posterior to the distal hypostomal setae. A study of transverse section of the hypostomal region (M) indicates that the dorsal wall of the hypostome (k′) articulates with the ventral wall of the hypostome (k) by means of a membrane (k″), indicating that the two walls can move independently of each other.

Hypostomal setae.—(Pl. I A, D) In both sexes the hypostomal setae are so arranged that each occupies the angle of a triangle, the longest side of which connects the distal and the lateral setae. None of the setae possesses setules. The distal (z_1), medial (z_2) and lateral (z_3) hypostomal setae in the male measure 135, 175 and 144 microns, respectively; those of the female measure 144, 184 and 107 microns, respectively.

Protosternum.—(Pl. I A, D, L, M; II) The protosternal region is bounded posteriorly by the deutosternum, laterally by the walls of the hypostome and the corniculi, and distally is continuous with the hypopharyngeal processes. Its wall is relatively thick and proximally provides the floor for the hypopharyngeal groove (M, y), the walls of which extend from the protosternum to the dorsal wall of the hypostome (k′).

Corniculi.—(Pl. I A, D, E, I; II) The horn-like corniculi (l) articulate with the distal wall of the hypostome and differ in the male and the female. In the female they measure 299 microns long and have smooth surfaces. In the male they are shorter (251 microns) and stouter. Their medial surface is concave; the ventral edge of this medial concave surface has two prominent teeth while its dorsal edge is smooth (I).

Salivary styli.—(Pl. I D, E, I, K, L; II) The salivary styli (f) of *M. ornata* are extremely long, curved structures which originate from the tentorial region just medial to the palpal trochanters. They measure about 400 microns long in the male and 316 microns long in the female. The salivary glands (f′) in stained preparations (K) show great concentrations of nuclei imbedded in a hyaline, homogeneous matrix.

Chelicerae.—(Pl. I B, C; II) The three-segmented chelicerae (a) of *M. ornata* are massive. Those of the male are larger than those of the female. In the female there are three teeth on the cutting edge of the immovable digit. On its lateral surface is a small seta just posterior to the most anterior tooth of the digit. There is also a small seta at the base of the digit on its dorsal surface. The synarthrodial membrane at the base of the digit is greatly expanded and encircling it posteriorly is a fringe of anteriorly projecting teeth. On the lateral surface of the second segment of the chelicerae just posterior to the movable digit is a large pore. The chelicerae of the male are characterized by a long, tightly coiled process which arises about midway from the lateral surface of the movable digit. It is called a "sperm carrying process" by Keegan and he compares it to the proboscis of a lepidopteran. The digit terminates in a curved, pointed tip and has one large, posteriorly curved tooth. The fringe of teeth are lacking at the base of the synarthrodial membrane, but as in the female the pore is present on the second segment. The immovable digit of the chelicerae of the male is irregularly dentate along its anterior half with about four teeth. The digit has a seta on its lateral surface just

posterior to the most proximal tooth but lacks the seta at its base, such as is present in the female.

Palps.—(Pl. I F) Designating the trochanter as number 2, the palpal segments range in size from large to small in the following order: 3:2:4:5:6. All of the palpal setae are nude. The trochanter has a large, horn-like tubercle on the anterior margin of its ventral surface; two setae project from its ventral surface. The more anterior of the two is the longer. The femur has 5 setae: 1 lateral, 1 medial and 3 dorsal. The most posterior of the dorsal setae is the longest on the femur. The genu has 6 setae: 1 lateral, 2 medial and 3 dorsal. The most posterior of the dorsal setae is the longest palpal setae. The more anterior of the two setae is the shortest seta on the genu. The tibia has 1 ventral seta, 3 lateral setae, 3 medial setae and at least 7 dorsal setae. The ventral seta is the most robust of the tibial setae; the three lateral setae are subequal in length; the most anterior of the medial setae is the shortest of the tibial setae and the most posterior of them curves sharply anteriorly. The most posterior of the dorsal setae is the longest seta on the tibia. From the anterior margin of the dorsal surface of the tibia is a curious seta. It is slightly shorter than the robust seta and instead of terminating in a sharp point its tip is blunt. The tarsus is characterized by the two-tined seta which projects from its medial surface. Just ventral to the base of the two-tined seta is another seta, shorter than either of the tines of the specialized seta. It is worthy of note because its base appears to be contiguous with that of the specialized seta. It is the only tarsal seta which arises from the same level on the tarsus as the two-tined seta. Perhaps this represents an intermediate condition prior to the three-tined tarsal seta characteristic of other species. The tarsus has at least 13 other setae: 2 ventral, 2 lateral and about 9 which are arranged in corona fashion on its dorsal surface. The more anterior of the ventral setae is the longest seta on the tarsus.

DISCUSSION

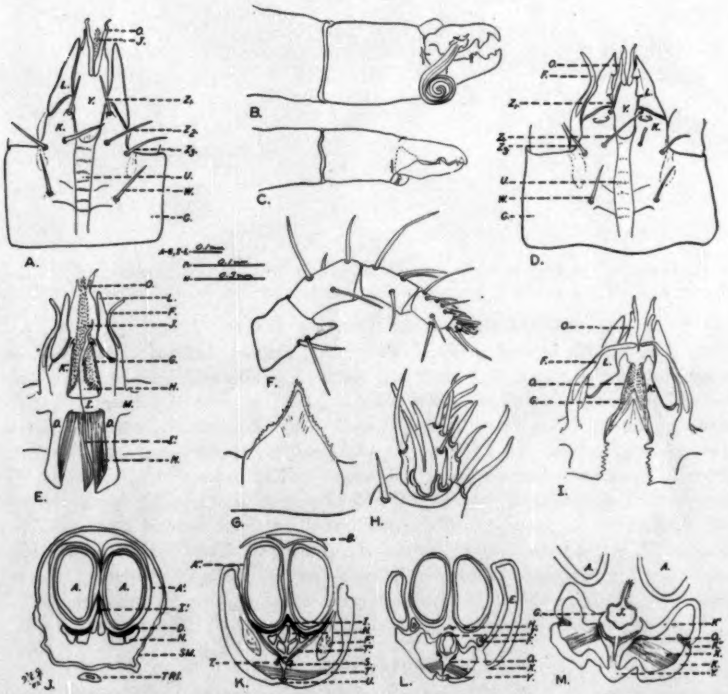
Megalolaelaps ornata presents several curious modifications that should be discussed. The most unusual of these is the absence of hypopharyngeal styli. It will be recalled that they originate at the junction of the wall of the hypopharynx with the dorsal wall of the hypostome and project dorsally over the epipharynx. Nothing can be said at this time about the significance of their absence since their function is not understood. One observation, however, which should be mentioned in relation with their absence is the space occupied by the labrum. Compared to the other mesostigmatid forms thus far studied in this survey, the labrum of *M. ornata* projects from a greater surface of the epistome, in fact, it spans the distance of its entire anterior surface and closes completely the hypopharyngeal region dorsally. The corners of the labrum reach the lateral junctions of the wall of the hypopharynx and the dorsal wall of the hypostome—the position from which the hypopharyngeal styli normally originate. Their absence may be in some way correlated with the development of the labrum. Sufficient forms have not yet been studied to establish this hypothesis.

Another modification, as mentioned earlier, is the lack of hypostomal processes. In *M. ornata* one of two things could have occurred: the hypo-

stomal processes have truly been lost or they have severed their association with the hypostomal region and appear detached. If this latter were true then the ventral portion of the hypopharyngeal process so designated here would be the hypostomal processes. An embryological study would be necessary to verify this.

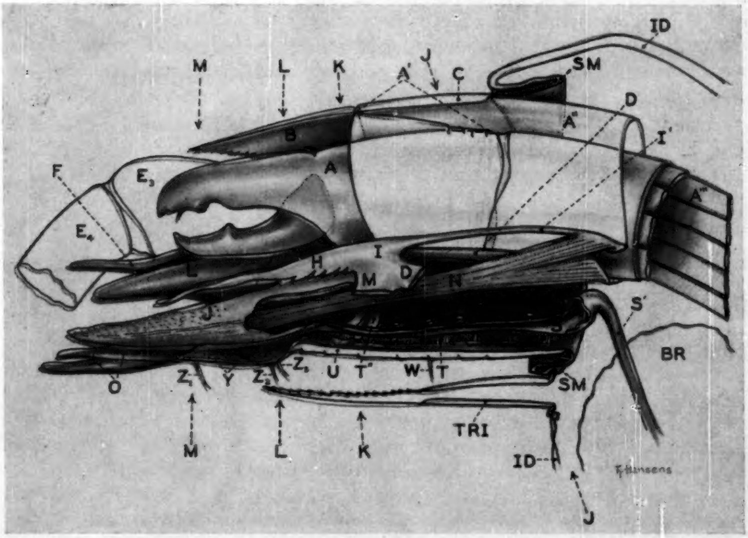
One last note of interest is the size of the salivary styli. They are unusually long in *M. ornata* and unlike those of *Pergamasus vargasi* do not originate from the dorsal surface but from the tentorial region and medial to the palpal trochanters.

PLATE I.



Gnathosomal structures of *M. ornata*.—A. Ventral view of female; B. Lateral view of chelicera of male; C. Lateral view of chelicera of female. D. Ventral view of male; E. Dorsal view of female with tectum, gnathosomal ring, chelicera and cheliceral sheaths removed; F. Lateral view of palp; G. Dorsal view of tectum; H. Detail of palpal tarsus, medial view; I. Dorsal view of male with tectum, gnathosomal ring, chelicerae, cheliceral sheaths, epistome, labrum and epipharynx removed; J. At level of origin of epipharyngeal muscles; K. At level of epistome; L. At level of origin of epipharynx; M. Detail of hypopharyngeal region. Sections from which figures J-M were taken were cut at 10 microns; stippling in figure M represents hypopharyngeal region.

PLATE II.



Reconstructed sagittal view of the gnathosoma of *M. ornata*.—Letters J, K, L and M refer to Pl. I and represent levels at which sections were cut. Legend same as for Pl. I.

ABBREVIATIONS USED IN PLATES

A, chelicera; A', internal cheliceral sheath; A'', external cheliceral sheath; A''', retractor muscles of chelicera; B, tectum. BR, brain; C, gnathosomal base; D, bar of subcheliceral plate; E, palp; E_3, femur of palp; E_4, genu of palp; F, salivary stylus; F', salivary gland; G, dorsal row of hypopharyngeal teeth; H, labrum; I, epistome; I', posterior epistomal process. ID, idiosoma; J, epipharynx; J', epipharyngeal base; K, hypostome; K'', membrane between dorsal and ventral wall of hypostome; L, corniculus; M, tentorium; N, epipharyngeal muscles; O, hypopharyngeal processes; Q, hypopharyngeal wall; S, pharynx; S', oesophagus; SM, synarthrodial membrane between gnathosoma and idiosoma; T, pharyngeal constrictor muscles. T', pharyngeal dilator muscles from gnathosomal ring; T'', pharyngeal dilator muscles from epistome; TRI, tritosternum; U, deutosternum; W, gnathosomal seta; X, hypopharyngeal dilator muscles; Y, protosternum; Z_1, Z_2, Z_3, distal, medial and lateral hypostomal setae.

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Comparison of the Gastropod Fauna in the Drainage Systems of Champaign County, Illinois

Ralph W. Dexter
Kent State University, Kent, Ohio

The writer has collected gastropods from the streams of Champaign County in east-central Illinois at various intervals since the fall of 1934. At that time he was introduced to the aquatic snail fauna of that region while on field trips with university classes conducted by Prof. V. E. Shelford and Prof. H. J. Van Cleave. In the spring of 1935 a survey of aquatic snails in the county was made under the direction of the latter. This study was continued in subsequent years whenever the writer found opportunity to revisit the area. Collections were made in the spring of 1945 and 1946, the fall of 1951, and the spring of 1952 and 1953. Specimens from the early collections were identified by Frank Collins Baker and Dr. N. T. Mattox. Later collec-

Fig. 1.—Map of Illinois showing location of Champaign County with its headwater streams.

tions were identified by the writer. In addition to those mentioned above I am indebted to Dr. John D. Mizelle, Dr. M. S. Ferguson, and Dr. D. H. Hansen for assistance in making field collections.

Champaign County is so located as to include the headwaters of the Salt Fork of the Big Vermilion River, the Little Vermilion, Embarrass, and Kaskaskia rivers, and much of the headwaters of the Sangamon River. A corner of the county drains to the Middle Fork of the Big Vermilion River whose headwaters are 20 miles northwest of its entrance into Champaign County. Because this area contains almost exclusively the headwaters of five different streams and all in close juxtaposition to each other, it is a good one for comparative study. The Middle Fork and the Salt Fork join to form the Vermilion

Fig. 2.—Map of Champaign County, Illinois, showing its watersheds.

River 11.5 miles east of the county and this continues eastward and southeastward to the Wabash River in Indiana. The Little Vermilion River likewise flows eastward to the Wabash River. The Embarrass flows south and then southeastward to the Wabash on the Illinois state line. The Kaskaskia River flows south, then southwestward to the Mississippi River. The Sangamon drains westward to the Illinois River. Eventually all tie into the Mississippi River system, but their mouths are widely separated (see figs. 1 and 2).

Champaign County is a nearly level upland plain containing 988 square miles. Its north-south axis is 36 miles long while its east-west axis is 27.5 miles long. This area was covered by the Illinoian and Early Wisconsin glaciers. The present drainage systems are for the most part bounded by terminal moraines of low rolling elevations. These systems within the county contain the following areas in square miles. Vermilion River, 415 (Salt Fork, 346 and Middle Fork, 69); Sangamon River 227; Kaskaskia River, 168; Embarrass River, 138; and the Little Vermilion River, 40 (Thompson and Hunt, 1930). The bottom type found in any certain place is dependent, of course, upon the velocity of the water. The larger streams have all types of bottom habitats — rubble, gravel, sand, and silt. The smaller ones contain largely sand and silt bottoms. Riffles and vegetation have developed in places where sedimentation has been undisturbed, but in a great many areas periodic dredging has removed vegetation and accumulated sediment to permit more effective drainage of this agricultural area. Annual rainfall averages 37 inches per year.

Many common species of fishes were found by Thompson and Hunt (1930) to inhabit certain drainages in Champaign County but not others. They wrote (p. 71), "Notwithstanding the close neighborhood of the headwaters of the different stream systems and the similarity of their habitats and of their drainage basins, the local distribution of their species is so restricted that 17 species are wanting in from one to five of the six stream systems of the

TABLE 1.—Comparison of the gastropods in the drainage systems of Champaign County, Ill.

Species	Middle Fork-Salt Fork of Vermilion	Sangamon	Kaskaskia	Embarrass	Little Vermilion
Physa gyrina	A	A	C	C	A
Fossaria humilis modicella	A	C	A	C	A
Ferrissia tarda	C	N	S	S	R
Helisoma trivolvis	C	N	N		C
Goniobasis livescens	C	+		R	A-shells
Lymnaea obrussa	N		S	R	
Campeloma rufum	N	S			
Pleurocera acuta	S	N			
Physa anatina	C				
Amnicola limosa	X			R	
Gyraulus parvus	+	+	R		
Pseudosuccinea columella			R		
No. of species collected	9	6	7	6	5
No. of stations sampled	12	9	12	12	6

Relative abundance is indicated as follows: A—abundant; C—common; N—numerous; S—scarce; R—rare; +—reported by Zetek; X—reported by both Zetek and Baker.

county." The writer set out to determine if this type of distribution was also true of the gastropod mollusks.

Collections were made with dip nets. For the most part samples were taken from the small and shallow drainages of the headwaters. Shoreline collecting was also carried out along the banks of the deeper main stream channels, especially at times of low water. Waters beyond wading depth were not sampled. Table 1 summarizes the findings of the writer.

Physa gyrina was the most abundant and widely distributed snail. It was found everywhere on mud, water weeds, and rocks. A closely related species, *P. anatina,* was found only in the drainage ditch of the Champaign sewage treatment plant, known as the Boneyard, which empties into the Salt Fork River. Probably it was an introduced species, but its isolated occurrence in this single drainage ditch of the county has never been explained. This species was studied by Brown (1935) and was identified by Dr. William J. Clench. Zetek (1918) reported *P. ancillaria* from Crystal Lake, a small impoundment in the Salt Fork system, after the Salt Fork had been dredged. Baker (1922) found *P. crandalli* from the same impoundment. Zetek (1918) also reported *P. sayi* in a stream nearby. (According to Wurtz, 1949, *P. ancillaria* and *P. sayi* are synonyms of *P. heterostropha.* Probably all of the specimens of *Physa* collected from this area actually are *P. gyrina* or *P. heterostropha.*)

Fossaria humilis modicella was also found in all drainage systems in abundance where it was widely distributed on mud banks. *Ferrissia tarda* was found in all drainages on rocks. This species was reported by Zetek (1918) from the Sangamon and from the Salt Fork before the ponding of Crystal Lake. After dredging of the Salt Fork, however, he found that this species had disappeared there and was replaced by *F. kirklandi.* He found that *Gundlachia meekiana* had likewise disappeared after the impoundment of Crystal Lake. Hoff (1940), as well as the writer, later found *F. tarda* again in this body of water and its drainage. Zetek also reported that specimens of *F. shimeki* from the Salt Fork were in the collections of the Illinois State Laboratory of Natural History, but he did not find it himself after a special search made for it.

Helisoma trivolvis, usually *H. t. pseudotrivolvis,* was found by the writer among vegetation and on rocks in all but the Embarrass River, where it was very possibly overlooked. *Goniobasis livescens* was found among gravel and on rocks only in the eastern watersheds, but Zetek (1918) found it in the Sangamon drainage as well. *Lymnaea obrussa* occupied the same habitat as *Fossaria humilis modicella,* but was not collected as abundantly or as widespread as that species. Closely related to these is *L. parva* which was reported from the Salt Fork drainage by Zetek and from both the Salt Fork and the Sangamon by Baker. Such a small species could easily be overlooked. Very possibly both *L. obrussa* and *L. parva* are present in all of these drainage systems. *Campeloma rufum* and *Pleurocera acuta* were collected in gravel from the larger streams only (Salt Fork of the Vermilion and the Sangamon), but possibly could have been taken from the other three drainages if collecting had been continued beyond the county line where those streams are more comparable to the others in size and habitats. Only the larger streams had riffle habitats of rubble and gravel and the swift currents which are associated with such bottom

materials. Specimens of *C. rufum* studied by Mattox (1935, 1938) and Van Cleave and Altringer (1937) were collected from the Salt Fork.

Three gastropods typical of pond habitats, *Amnicola limosa, Gyraulus parvus,* and *Pseudosuccinea columella,* were found in the shallow waters of two of the streams where the current was slow and vegetation had become established. Zetek (1918) found *Menetus exacuous, Pomatiopsis lapidaria, Gyraulus parvus, G. deflectus,* and *Amnicola integra* (= *A. cincinnatiensis*) in addition to *A. limosa* in a similar habitat at Crystal Lake which flows into the Salt Fork River. *G. parvus* was found in both the Salt Fork and Sangamon drainages. Baker (1922) also found *A. integra* in the Salt Fork system. As pond conditions develop from accumulation of sediments and establishment of rooted plants, or are created artificially by impoundments, the snail population, along with other elements of the fauna, changes from the fluviatile to the pond-type.

Zetek found *Valvata bicarinata* on water lilies in slowly moving waters of the Salt Fork system near St. Joseph and reported that the collections of the Illinois State Laboratory of Natural History contained specimens of *Lymnaea palustris* found in a creek which joins the Salt Fork at St. Joseph.

Baker (1922) found *Pomatiopsis lapidaria* abundantly in small, cold streams flowing into the Sangamon and later (1931) reported it from a similar situation in the watershed of the Salt Fork. Dexter (1953) found this species in temporary pools on the flood plain of this stream, but not in the river itself or its tributaries.

The unstable taxonomy of many of the aquatic gastropods which have been collected in Champaign County, and the continuously disturbed conditions of the streams from pollution, erosion, dredging, and ditching, make a study of their geographical distribution a difficult one. It is clear, however, that unlike the situation found in the fish survey of this county and often found with certain bivalves and land snails, there is no significant difference in the aquatic gastropod fauna of the five different drainage systems of the county even though they have no direct connection with each other. When compared ecologically habitat by habitat, the watersheds of this county, consisting largely of headwater streams, contain essentially the same common species of gastropods. Only one common species, *Physa anatina,* has a restricted distribution, and that one may not be a native species. Dexter, Swart, and Davis (1951) found the same situation in adjacent but separate drainage systems of Lake Erie and the Ohio River in northeastern Ohio. Probably dispersal factors other than stream connections such as aquatic birds and mammals are responsible for the general distribution of the common gastropods of these streams.

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A Field Study of Wild Mammals and Fleas of Santa Fe County, New Mexico

R. Holdenried and Harvey B. Morlan

Communicable Disease Center, Public Health Service, U. S. Department of Health, Education, and Welfare, Atlanta, Ga.

Determination of feasible methods for limiting the transfer of such diseases as plague and tularemia from wild rodents to man requires basic biological information obtained through intensive field study of rodents and their associated ectoparasites. The collection of such information was a primary objective of the Santa Fe Field Station which was established in July 1951 as a part of the plague investigative program of the Communicable Disease Center. The present report has been prepared to give general background information for more detailed papers on specific phases of the study. The background information consists of a concise, integrated view of the area, methods of study, and species of mammals investigated. For each species of mammal, observations are given on reproduction, local distribution, and general abundance of the most frequently collected species of fleas. Subjects expected to be presented in more detailed reports include: natural history of the most extensively studied species of rodents; seasonal, host, and geographical distribution of ectoparasites; and susceptibility of rodent species to plague organisms. An excellent review of published studies on plague in wild rodents has been presented by Pollitzer (1952).

Acknowledgments.—Medical Director Vernon B. Link provided guidance in formulating plans for establishment of the Santa Fe Field Station. Other Public Health Service personnel who contributed advice and encouragement included: Assistant Surgeon General Justin M. Andrews; Scientist Director S. W. Simmons; Senior Sanitarian (R) Frank M. Prince; Bacteriologist Stuart F. Quan; and Entomologist Harold E. Stark. Much of the field work was accomplished by Research Biologists Huey C. Owen and John S. Adams.

Specialists who have generously made mammal identifications are: Drs. Robert T. Orr, California Academy of Sciences; E. Raymond Hall and his associates at the Museum of Natural History of the University of Kansas; and Donald F. Hoffmeister, Museum of Natural History of the University of Illinois. Dr. Hoffmeister also visited the field station to contribute aid in the problem of distinguishing the five species of *Peromyscus*.

The account of soils is based on an unpublished report entitled "First Inspection Report, Pojoaque Soil Conservation District, Santa Fe County, New Mexico," prepared by Division of Soil Survey, Bureau of Plant Industry, U. S. Department of Agriculture.

A collection of identified herbarium specimens of flowering plants growing at the airport was perpared by Mr. Joseph W. McKinley, Jr. while he was associated with the station during the summer of 1953.

Area of Study

A map presented by Link (1951) shows the counties in United States from which mammals and/or ectoparasites have been tested for plague and the counties from which material infected with plague organisms was obtained. South Dakota and Nebraska are the only states extending west of longitude 100° in which the disease has not been found.

Suitable conditions for a field study could have been found in several of these states. However, attention was directed toward New Mexico by Link's (1950) report of five

recently diagnosed cases of human plague and recovery of plague organisms from ectoparasites and/or their mammal hosts in 19 of New Mexico's 32 counties. An additional case of human plague occurred in New Mexico in January 1951 (Pub. Health Rept., 1951).

Several factors, considered desirable for a field study relative to rodent disease, were possessed by an area near Santa Fe in north central New Mexico. Important features of this area included 1) a recent (1950) case of human plague, 2) recent active rodent plague had been indicated by recovery of plague organisms from fleas from white-footed mice in 1951, 3) a relatively undisturbed area at the Municipal Airport for rodent life history studies, and 4) convenient access to Upper Sonoran, Transition, and Canadian Life Zones for comparative study of the associated mammal and ectoparasite fauna.

The area selected for study (fig. 1) was limited to Santa Fe County between Ranges

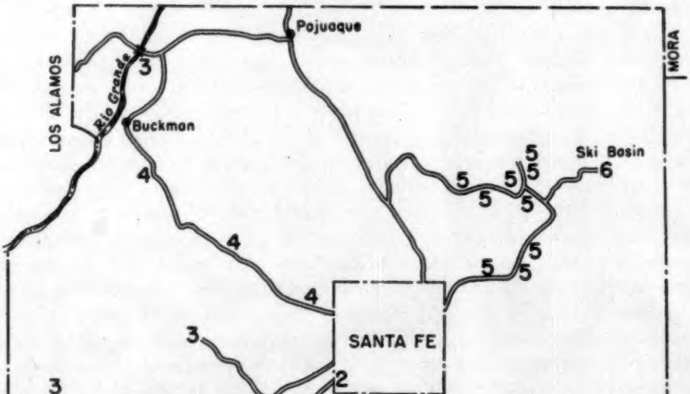

Fig. 1.—Map of the Santa Fe Field Station study area, Santa Fe County, New Mexico. Trapping locations, usually adjacent to roads, are indicated with figures; identical figures designate similar mammal habitats.

7 to 11 East and Townships 12 to 20 North, New Mexico Principal Meridian. The city of Santa Fe is east of the Continental Divide at 35° 41′ 11″ North Latitude, 105° 56′ 10″ Longitude west of Greenwich. With one exception, all collections were made within 22 miles of Santa Fe. One trapping location (No. 7 of Fig. 1) was about 34 miles south of Santa Fe. Most of the study area slopes west and south toward the Rio Grande with lowest elevations of about 5,500 feet above sea level. The river in its narrow scoured stream bed has little direct influence on the terrestrial rodents. Different trapping locations have been plotted (fig. 1) with the use of numerals. Different locations that have been designated with identical numerals were considered to constitute similar types of habitats that may be characterized as follows: (1) Located southeast of Santa Fe along the base of the Sangre de Cristo Mountains which here are composed of granite, schist and quartzite, the area included the lower edge of the Transition Zone and the upper margin of the Upper Sonoran Zone. With increasing elevations the mixed growth of one-seed juniper [*Juniperus monosperma* (Engelm.)] and piñon pine (*Pinus edulis* Engelm.) give way to mixed piñon pine and yellow pine forest. (2) Includes the most intensively studied Municipal Airport area and contains gently rolling grassland with junipers restricted to ridges and hill slopes. The principal grasses in this portion of the Upper Sonoran Zone are *Hilaria Jamesii* (Torr.) and *Bouteloua gracilis* (H.B.K.) but many other grass and herbaceous species are present. Cane cactus [*Opuntia imbricata* (Haw.) D.C.] is widely scattered in the area. The area, formerly a plain, has been reduced through erosion to a series of mesas and "bad lands." Soft consolidated sandstones to slightly consolidated loams, sandy loams, and heavier textures are overlain by a mantle of gravelly alluvium largely derived from the igneous complex of the Sangre de Cristo Mountains. The calcareous soil, predominantly brown to yellowish or grayish brown, varies in texture from sandy clay loam through sandy loam to loam. (3) Also in the Upper Sonoran Zone, the soils are generally shallow and bouldery with many lava boulder outcrops. A few low, old volcanic cones rise above the gently rolling plain. Principal plant cover is similar to (2) above. (4) Located north of Santa Fe, the area consists of juniper and piñon pine-covered ridges bordering narrow valleys which are subject to flooding following summer thunderstorms. Soils are as described for (2) above. (5) Yellow pine (*Pinus ponderosa* Lawson), white fir [*Abies concolor* (Gordon and Glendinning)], Douglas fir [*Pseudotsuga taxifolia* (Pair.) Britton], and scrub oak (*Quercus* sp.) are the chief trees in this primarily forest-covered Transition Zone on the western slope of the Sangre de Cristo Mountains. (6) Quaking aspen (*Populus tremuloides* Michx.) and blue spruce (*Picea pungens* Engelm.), together with both white and Douglas fir, form the forests at the lower elevations of this Canadian Zone area while forests of pure Engelmann spruce (*Picea Engelmanni* Parry) as well as aspen grow in the upper limits of the zone. Mammals were collected in locations up to 11,000 feet in the open meadow and in the surrounding Engelmann spruce forests of the Santa Fe Ski Basin. Limited areas of Hudsonian and Alpine Life Zones exist on the highest elevations above the area included in the present study. (7) A single collecting trip was made to this Upper Sonoran Zone area in the San Pedro Mountains at an elevation of from 6,800 to 7,500 feet.

The area of intensive study in the Santa Fe Municipal Airport at an elevation of about 6,300 feet includes the following portions of Township 16 North, Range 8 East, New Mexico Principal Meridian: southern portions of sections 9 and 10, northern portion of section 15, northern and western portions of section 16. The airport, since it was fenced in 1943, has been free of grazing. The central mesa, about 1¼ miles wide, has been somewhat leveled for the runways and taxiways. The central mesa slopes steeply down about 40 feet on the northwest side to the Santa Fe Creek plain. A similar sharp break occurs on the southeast side. The land near Santa Fe Creek is nearly covered with small waterworn stones.

Two areas were intensively studied at the airport. One area of approximately 66 acres (4,100′ x 700′), on the Santa Fe Creek plain, contained mostly herbaceous plant growth which included nine perennial grass species. Scattered rabbit brush [*Chrysothamnus nauseosus* (Pall.)] up to 3 feet high, an occasional one-seed juniper bush usually less than 10 feet high, scattered cane cactus and occasional clumps of apache plume [*Fallugia paradoxa* (D. Don)] were the most conspicuous woody plants. The second area adjoined a corner of the first area and was 7,300 feet long, varying from 200 to 800 feet in width. The distance between opposite ends of the two areas was 11,400 feet. The second area, selected because it provided white-throated woodrats (*Neotoma albigula*) and three species

of white-footed mice (*Peromyscus*) which were only occasionally present on the first area, included short deep ravines cutting the steep slope between the airport mesa surface and the Santa Fe Creek plain. On the ridges between ravines small clumps or scattered plants of one-seed juniper up to 12 feet high were occasionally interspersed with patches of yucca (*Yucca glauca* Nutt.). Flatter grassland surrounded the bushy growth.

The following climatological data for Santa Fe, with temperatures in degrees Fahrenheit were taken from the United States Department of Agriculture (1941) which summarized 40 years of observations. The semiarid climate varied in daily mean temperatures from 29.2°F in January to 68.9°F in July. The yearly minima temperatures averaged —13°F while the yearly maxima averaged 97°F. The sun shone 70 to 80 per cent of the possible time. Relative noontime humidities usually varied from 35 to 45 percent and remain low even during the months of heaviest rainfall. Rainfall averaged 14.19 inches per year with from 10 to 12 inches, or about 78 percent of the total, falling in the April to September plant-growing season. The summer rains, which resulted from thunderstorms, occurred as heavy downpours of short duration over limited areas. Because of the short duration of the storms, water seldom penetrated more than a few inches of soil. High ground temperature and low air humidity contributed to rapid evaporation and drying of the soil. At the lower elevations snowfall was light, usually melting within a few days after falling. At the higher elevations the fall was considerably heavier with some snow usually present from November to June. Winter storms were also brief and the sun shone 80 percent of the possible time. Winds were frequent, especially from March through May, and caused much of the surface soil erosion.

METHODS

Mammal life history data, obtained primarily through observation of trapped live rodents were supplemented by field notes of observed tracks, middens, burrowing activity, food storage, study of carcasses, etc. Most live-trapped animals lived on the airport and were obtained by trapping at permanent marked locations on a once-a-week schedule. Live catch traps of three different types, described by Holdenried (1954), and snap traps were set at places most likely to catch animals, i.e., at burrow entrances for burrowing rodents and at openings in stick houses for the house-dwelling woodrats. Areas other than the airport were also repeatedly live-trapped for special studies. Diurnal species were usually released on day of capture but nocturnal species were left overnight in the field when minimum temperatures remained above freezing; in winter the trap lines were inspected between 8 and 11 p.m. All trapped animals were then brought to the laboratory and vacant traps were sprung. The following morning the captured mammals were examined and notes on age, sex, weight and other pertinent data recorded. Ectoparasites were removed as scheduled to secure representative samples. Live mammals were rarely anesthetized and ectoparasites were removed while alive. Fleas were obtained while the host was held over a pan with sides 8 inches high. Fleas usually dropped into the pan as the collector blew into the host's hair. Others were removed with forceps. Ticks, lice, and unattached mites were removed with forceps. Attached chiggers were obtained in pieces of skin scraped from infested areas. Collections of ectoparasites from live mammals were of a consistent degree of completeness to provide reliable indication of seasonal changes in abundance. Following the removal of parasites, each mammal, if unmarked, was marked by a combination of clipped toes and was then returned to the location of its capture and released.

Animals held captive in traps for up to 18 hours away from their homes in the dry atmosphere and at variable temperatures were undoubtedly adversely

affected. The degree of this disturbance was not measured, but limited hindrance was indicated by repeated recapturing of individuals over long periods. Evans and Holdenried (1943), studying the relation of ground squirrels *(Citellus beechyi)* to plague used successfully a similar recapturing procedure.

Mammal carcasses were obtained from areas other than the airport, through the use of break-back traps and shooting. Dead mammals, placed in cloth bags, were exposed to hydrocyanic acid for about 15 minutes until ectoparasites were killed. Dead ectoparasites were then removed from their hosts through brushing and the use of forceps and held in 2% saline solutions. Depending on the need of the program, parasites were identified and sent to the laboratory of the San Francisco Field Station for bacteriological tests for plague organisms, were preserved for further taxonomic study or were discarded. The mammal carcasses following identification, were examined for gross pathology and evidence of reproduction. Occasionally the food in trapped mammal's stomachs was examined and identified. For each mammal species studied, at least one and usually more conventional museum specimens consisting of skull and mounted skin were prepared. One or more specimens of each species were sent to museums for identification by specialists in the various mammal groups. These specimens will be deposited at the California Academy of Science and the Museum of Natural History of the University of Kansas.

RESULTS

Routine identification of ectoparasites was continued from July 1951 to February 4, 1954. The 8,784 mammals examined (or re-examined) for ectoparasites in this period resulted in the collection of over 26,000 fleas representative of 51 species. Other collections from rodent nests and a bird added three additional species of fleas, for a total of 54 species presently known to occur in Santa Fe County.

By February 4, 1954, 4,900 individual mammals had been trapped by the Field Station staff. Over one-half (2,587) of the individuals were captured 12,981 times on the airport study area; the remainder were taken in the special search for plague or for other studies. The approximate total of 40,000 trap settings resulted in about 16,000 captures. Many of the species encountered were on or within a few miles of the geographic limits of their range and some were recorded for the Santa Fe area for the first time.

For each species of mammal in the following list, observations are given on local distribution, reproduction, and abundance of the most frequently collected species of fleas. Detailed data on complete flea-host relationships and seasonal changes in abundance are not considered in the present report. The epidemiological significance of the most prevalent species of fleas is potentially great; definitive determination of actual significance is dependent upon more knowledge than is presently available.

Sorex obscurus obscurus Merriam.—Two dusky shrews were captured in the lower edge of the Transition Zone in location 5, and 3 were taken in location 6.

No ectoparasites were found.

Corynorhinus rafinesquii pallescens Miller.—Five male and one very fat female western big-eared bats were collected February 4, 1954, about 200 yards inward from the entrance of an abandoned mine shaft at location 7. The torpid bats were scattered along the roof of an 8- to 10-foot high tunnel.

The six bats were free of fleas.

Ochotona princeps incana Howell.—Pikas were numerous on the granite talus slopes at location 6. In October of 1952 and 1953, 3 half-grown young weighed from 65 to 107 g while 2 adult females taken at the same time weighed 164 and 165 g. When the area was visited in January 1954, all pika-inhabited talus slopes were covered by snow with only a few of the largest boulders protruding. There were no pika tracks on the snow surface. In early February 1954, on a warm quiet day, pikas were seen on top of some of these large boulders which may be used even at this season for "lookouts" and as places to sun-bathe.

Of 9 conies examined, 3 were infested with 12 fleas of *Ctenophyllus terribilis* (Rothschild) and 2 with 6 *Amphalius necopinus* (Jordan).

Lepus californicus texianus Waterhouse.—Blacktail jackrabbits were particularly noticeable in the open flat land of location 2.

Only 4 jackrabbits were examined for ectoparasites; 2 were infested with 7 fleas of *Hoplopsyllus affinis* (Baker) and 1 with 5 *Cediopsylla inaequalis inaequalis* (Baker).

Sylvilagus audubonii warreni Nelson.—The desert cottontail was widespread in the rabbit brush and among junipers of locations 1, 2, 3 and 4 and was locally abundant particularly among the junipers at the airport.

Of 170 rabbits examined, 135 were infested with 3,175 fleas of *Hoplopsyllus affinis,* and 128 with 2,392 *Cediopsylla i. inaequalis.*

Tamiasciurus hudsonicus mogollonensis (Mearns).—Spruce squirrels were collected in the upper limits of the Transition Zone in location 5 and also in both blue and Engelmann spruce forests of the Canadian Zone in location 6.

Of 9 squirrels examined, only 1 was infested with a single flea of *Monopsyllus vison* (Baker); however, examination of 4 nests resulted in collection of 28 fleas of this species as well as 25 of *Tarsopsylla coloradensis* (Baker) and 16 of *Orchopeas c. caedens* (Jordan).

Marmota flaviventris obscura Howell.—On August 5, 1953, an adult female and an adult male, yellowbelly marmots weighing 3,289 and 5,046 g respectively together with 2 immature females weighing 1,115 and 1,156 g were collected from an isolated rock pile in location 6; all individuals had large fat accumulations. Another marmot was shot on August 13, but when the area was next visited on October 5 none was seen and apparently all remaining were in hibernation.

All of 6 marmots examined were infested with a total of 44 fleas of *Thrassis stanfordi* Wagner.

Cynomys gunnisoni zuniensis Hollister.—Following discontinuance of a cooperative prairie dog control campaign by Santa Fe City and County, New

Mexico Health Department and the U. S. Fish and Wildlife Service in 1950, these rodents have again increased noticeably in abundance. Colonies exist in locations 1, 2, 3, and within the city of Santa Fe. In the colony studied, live-trapped females were noticeably pregnant in early May. Young were born by the end of the month. Some young appeared about the burrow mouths in early June. All individuals entered hibernation in October, 1951, and 1952 but in 1953 a few did not hibernate until the first week in November. In each year they reappeared above ground early in March.

Of the 134 prairie dogs examined, 75 were infested with 571 fleas of *Opisocrostis hirsutus* (Baker) and 26 with 352 of *O. tuberculatus cynomuris* Jellison.

Citellus spilosoma marginatus Bailey.—The spotted ground squirrel was widespread in locations 1 and 2, living even in vacant lots in the town of Santa Fe.

Of 326 squirrels examined, 177 were infested with 719 fleas of *Thrassis pansus* (Jordan).

Citellus variegatus grammurus (Say).—The rock squirrel, although nowhere abundant, was widely distributed over all of the Santa Fe area below the Transition Zone. Some individuals were active throughout the year. A rock squirrel with 5 embryos was trapped in April, and quarter-grown young were taken in June.

Only 9 rock squirrels were examined for ectoparasites; 7 were infested with 48 fleas of *Hoplopsyllus anomalus* (Baker), 6 with 43 of *Diamanus montanus* (Baker).

Citellus lateralis lateralis (Say).—Golden-mantled squirrels were particularly abundant along the open slopes of location 6. All individuals at this high elevation had gone into hibernation by the last week in September 1953, but at a lower elevation in location 5 one was captured when the ground was slightly snow-covered on November 5.

Of 29 squirrels examined, 3 were infested with 3 fleas of *Diamanus montanus* and 3 with 3 of *Oropsylla idahoensis* (Baker).

Eutamias minimus operarius Merriam.—Least chipmunks were captured from the lower limit of the Transition through the Canadian Zone. They reached their greatest abundance in location 6, but undoubtedly also inhabited the higher mountain crests. Least chipmunks were active in early October after golden-mantled squirrels and marmots had begun hibernation.

Of 19 chipmunks examined, 6 were infested with 8 fleas of *Monopsyllus eumolpi* (Rothschild).

Eutamias quadrivittatus quadrivittatus (Say).—Below the central portion of the Transition Zone, wherever tree, brush or rock cover was sufficient, the Colorado chipmunk was captured. They have been taken in both northern and southern portions of location 3, southern portions of locations 2 and 1. Two lactating individuals were taken in April, one with 6 and the other with 4 placental scars. An April captured male had large testes in scrotal position and cauda epididymides tubules macroscopically visible. Jameson (1950)

used macroscopically visible tubules of the cauda epididymides of *Peromyscus* as one criterion of fecundity. It is probably a good criterion for some other rodent species including chipmunks.

Of 88 chipmunks examined, 28 were infested with 53 fleas of *Monopsyllus eumolpi*.

Thomomys talpoides fossor Allen.—Specimens of the northern pocket gopher were taken from 8,500 to 10,500 feet elevation but neither the upper nor lower range limit was determined. All *T. talpoides* were taken from August through November, mostly in October. None appeared to be in breeding condition.

Of 15 gophers examined, 14 were infested with 77 fleas of *Foxella ignota* (Baker).

Thomomys bottae pervagus Merriam.—Valley pocket gophers were absent or rare over most of their range in the Upper Sonoran Zone. Specimens were captured only in the city of Santa Fe.

Of 6 gophers examined, 4 were infested with 38 fleas of *Foxella ignota.*

Perognathus flavus flavus Baird.—The silky pocket mouse was present in both locations 1 and 2. It was very numerous on the airport trapping area. The pocket mice were live-trapped throughout the year but were rarely taken in break-back traps. Seventy-seven pregnancies were recorded by months as follows: January 0, February 2, March 0, April 11, May 10, June 29, July 8, August 1, September 10, October 6, November and December 0. Reproductive activity was most intense from April through June and nearly absent from November through March.

Of 989 mice examined, 137 were infested with 184 fleas of *Meringis jamesoni* Hubbard.

Dipodomys spectabilis baileyi Goldman.—East of the Rio Grande, the northern limit of the bannertail kangaroo rat is given on a distributional map by Bailey (1931) as 34 miles south of Santa Fe near Algodones. At the present time, however, this rat occupies much of the grassland extending northward about 2 miles beyond Santa Fe, and as far east as Lamy. Specimens have been taken in locations 1, 2, 3 and 4. Near Santa Fe, in addition to currently used burrows, there were well-weathered low earth mounds, obviously remains of the characteristic large mounds of dirt excavated from burrows by bannertail kangaroo rats. The weathered mounds must have originally been built well over 10 years ago. These rats probably have been present in the Santa Fe area for many years and are not a recent addition to the fauna. All of the 27 recorded pregnancies occurred from January through May with the largest number (8) in March.

Of 1,128 rats examined, 792 were infested with 6,244 fleas of *Meringis rectus* Morlan and 462 with 3,184 *M. nidi* Williams and Hoff.

Dipodomys ordii medius Setzer.—The Ord kangaroo rat, generally present over all of the Upper Sonoran Zone with the exception of the denser juniper-piñon pine stands, was locally one of the most abundant rodents. With the exception of December, some pregnant *D. ordii* were captured in every month.

A total of 154 pregnancies were recorded, and percentages of the total were computed by months as follows: January 7, February 21, March 20, April 19, May 11, June 6, July 1, August 2, September 8, October 3, November 1, December 0.

Of 2,232 rats examined, 260 were infested with 364 fleas of *Meringis nidi* and 191 with 267 *M. parkeri* Jordan.

Reithrodontomys megalotis aztecus Allen.—Western harvest mice were captured in largest numbers near Lamy (location 1) but occasional specimens have been taken also in locations 2 and 3. All of the 10 pregnant harvest mice were captured from January through July. In addition, 3 males in April and 2 in May had cauda epididymides tubules clearly visible. Insufficient numbers were taken in other months to define the breeding season.

Of 130 harvest mice examined, 27 were infested with 59 fleas of *Orchopeas leucopus* (Baker).

Peromyscus maniculatus rufinus (Merriam).—Deer mice were continuously present from the lowest elevations along ridges with scattered junipers where they frequently associated with *P. leucopus* and *P. truei*, to the highest elevations in dense forests and open meadows of location 6. In July, August, and September pregnant deer mice were captured only at the higher elevations in locations 5 and 6. There was no indication of repreduction in October and November, but pregnant mice were captured at lower elevations in each month from December through June.

Of 445 mice examined, 89 were infested with 168 fleas of *Monopsyllus wagneri* (Baker), and 76 with 138 of *Orchopeas leucopus*.

Peromyscus leucopus tornillo Mearns.—On the low, rounded ridges with scattered junipers and along rocky prominences below 7,000 feet elevation, the white-footed mouse was taken. Among the capture locations for this mouse was one in location 4, 6 miles North and 7 miles West of Santa Fe, which represented its northern range limit in central New Mexico. For this mouse, two breeding periods were apparent (table 1), one from January through May, and a second, less intense period from August through September.

Of 285 mice examined, 98 were infested with 214 fleas of *Orchopeas leucopus*, and 82 with 192 of *Monopsyllus wagneri.*

Peromyscus boylii rowleyi (Allen).—Brush mice were taken in locations 1, 3, and 5, in dense brush usually broken by boulders or trees and also among scattered junipers on nearly bare rocky ground. Reproductive records for brush mice are insufficient to indicate seasonal activity. One pregnancy occurred in March, another in August and males with large cauda epididymides tubules were recorded in April.

Of only 27 mice examined, 5 were infested with 6 fleas of *Monopsyllus wagneri,* and 4 with 6 of *Malaraeus sinomus* (Jordan).

Peromyscus truei truei (Shufeldt).—Piñon mice were the most numerous and widespread of the *Peromyscus* species in the Upper Sonoran Zone. They were not, however, inhabitants of the open grassland but were most abundant

along rocky cliffs and ridges supporting junipers. Like *P. boylii* and *P. nasutus* they ranged up to the lower edges of the Transition Zone tongues which protrude into the Lower Sonoran Zone along canyon bottoms. Piñon mice may breed throughout the year, but most of the reproductive activity occurs in the April-June period. Few young were produced from October through February.

Of 662 mice examined, 260 were infested with 578 fleas of *Orchopeas leucopus* and 203 with 507 of *Monopsyllus wagneri.*

Peromyscus nasutus nasutus (Allen).—Specimens of rock mice were taken not only among boulders and rocky cliffs but also in brush. They were captured in locations 1, 3, and 5. In January, April, May, and August the reproductive organs of 40 rock mice were examined for evidence of fecundity. Cauda epididymides tubules were enlarged and visible in some males in each of these months. The only pregnant female was taken in August. Immature individuals formed a part of the catch in each of the four months in which these mice were captured.

Only 21 mice were examined; 2 were infested with 4 fleas of *Monopsyllus wagneri.*

Onychomys leucogaster pallescens Merriam.—Northern grasshopper mice were of scattered occurrence in the open grassland and were captured only in locations 1, 2, and 3. A total of 16 pregnant grasshopper mice were examined, all in the period from March through September. April was the month with the largest number (6) of pregnant mice.

Of 405 mice examined, 128 were infested with 368 fleas of *Monopsyllus exilis* (Jordan). Fleas, more common to the kangaroo rats and spotted ground squirrels, were often collected from grasshopper mice.

Neotoma micropus canescens Allen.—In the Santa Fe area, the southern plains woodrat is largely dependent on cane cactus *(Opuntia imbricata)* for food. Trips of one hundred yards or more over open exposed ground were sometimes required to obtain the cactus. The southern plains woodrats were scattered over the Upper Sonoran Zone. No pregnancies were observed in February, October, and November. Twenty-seven recorded pregnancies were fairly evenly distributed over 9 months (table 1). More extensive observations may indicate reproductive activity in varying degree throughout the year.

Of 579 rats examined, 451 were infested with 3,801 fleas of *Orchopeas sexdentatus* (Baker).

Neotoma albigula albigula Hartley.—In contrast to *N. m. canescens,* the white-throated woodrat rarely used cacti but depended on juniper for forage and for support of its stick houses. The two species were frequently closely associated and sometimes alternately used a single house. The white-throated woodrat was taken in the lower portion of location 6 and was generally distributed among the junipers in locations 1, 2, 3, and 4 in the Upper Sonoran Zone. White-throated woodrats exhibited some reproductive activity throughout the year with most females becoming pregnant in March, April, and May. Of the 47 recorded pregnancies, 24 occurred in this period, (March

to May). Smallest numbers of young were produced in the period from September through December.

Of 981 rats examined, 305 were infested with 782 fleas of *Orchopeas sexdentatus*.

Neotoma mexicana fallax Merriam.—The Mexican woodrat was found only along rock cliffs and among boulders in locations 1, 3, and 5. It was frequently in association with the white-throated woodrat. Records of reproductive activity of the Mexican woodrat were insufficient to indicate degree of seasonal intensity. One pregnancy was recorded in April and another in August. Englarged cauda epididymides tubules were noted once in March and once in August. Two immature specimens were taken in August.

Only 9 rats were examined; 4 were infested with 20 fleas of *Orchopeas neotomae* Augustson, and 3 with 26 fleas of *Stenistomera alpina* (Baker).

Neotoma cinerea orolestes Merriam.—Bushytail woodrats were taken in locations 5 and 6 only. Both of 2 rats examined were infested with 20 fleas of *Orchopeas sexdentatus*.

Clethrionomys gapperi guati Cockrum and Fitch.—Four boreal redback voles were captured in a dense Engelmann spruce forest in location 6. Deer mice and spruce squirrels were the only other rodents taken in the immediate vicinity.

Only 2 fleas were collected; 1 of *Rectofrontia fraterna* (Baker) and 1 of *Malaraeus euphorbi* (Rothschild).

Microtus longicaudus mordax (Merriam).—Probably the longtail vole was most abundant in the high mountain meadows but they were captured also on dry pine and scrub oak covered hillsides in the lower edge of the Transition Zone in location 5. Voles were trapped only in April, August, October, and November. Pregnancies were noted in April and August. In October 8 out of 11, and in November 9 out of 11 of the trapped voles were immature.

Of 41 voles examined, 6 were infested with 10 fleas of *Peromyscopsylla hamifer vigens* (Jordan).

Zapus princeps princeps Allen.—Only two western jumping mice were captured. Both individuals were taken from along a small stream densely covered with white fir, yellow pine, quaking aspen and common choke-cherries *(Prunus virginiana L.)* at about 8,000 feet elevation in location 5.

No ectoparasites were found.

Mustela frenata nevadensis Hall.—An adult male was captured at 11,000 feet elevation in a pile of loose boulders in location 6. This longtailed weasel showed little concern for man and was captured within 5 minutes after the trap was set, while his captor stood in full view about 30 feet away.

No ectoparasites were found.

Mustela frenata neomexicana (Barber and Cockerell).—An adult female of this subspecies was killed by a car on a road near the airport. A male, killed by dogs, was obtained 11 miles Southwest of Santa Fe, in location 2. None

was seen alive in many hundreds of man-hours spent in the field and their tracks were rarely found. Weasels were apparently not abundant.

No ectoparasites were found.

DISCUSSION

Pregnancy records of 12 mammal species, all inhabitants of the Upper Sonoran Zone, were sufficiently extensive to indicate limits of periods of reproductive activity (table 1). The time of reproductive activity for the species is possibly accompanied by stress resulting from the search for mates and the females' burden of pregnancy and lactation. All species observed, even those with extended reproductive periods, produced young most prolifically from February through June. Many young became independently active early in summer producing peak population densities. Conditions appear to be most favorable in the first half of the year for diseases dependent upon large numbers of young mammals and the associated increased population pressures combined with the presence of adults under the stresses accompanying reproductive activity.

TABLE 1.—Occurrence of mammal pregnancies from July 1951 through February 1954, Santa Fe County, New Mexico.

Species	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
Sylvilagus audubonii	00	00	00	....	....	....	....	00	00	00	00	00
Cynomys gunnisoni	—	—	00	00	....	00	00	00	00	—	—	—
Citellus spilosoma	—	—	—	00	....	....	....	....	00	00	00	—
Perognathus flavus	00	....	00	....	....	....	....	....	....	....	00	00
Dipodomys spectabilis	....	....	....	....	....	00	00	00	00	00	00	00
D. ordii	....	....	....	....	....	....	....	....	....	....	....	00
Peromyscus maniculatus	....	....	....	....	....	....	....	....	....	00	00	....
P. leucopus	....	....	....	....	....	00	00	....	....	....	00	00
P. truei	....	....	....	....	....	....	....	....	....	00	....	00
Onychomys leucogaster	00	00	....	....	....	....	....	....	....	00	00	00
Neotoma micropus	....	00	....	....	....	....	....	....	....	00	00	....
N. albigula	....	....	....	....	....	....	....	....	....	....	00	....
No. of species pregnant	7	7	8	10	12	9	9	9	8	4	2	3

00 = no pregnancies; .... = pregnancies; — = no records, species not trapped.

Solution of many problems regarding the perpetuation of plague in nature will require much further investigation. Table 2, which lists the most commonly collected mammals and fleas, provides a general view of the numerically most important potential vectors of rodent-borne disease in the vicinity of Santa Fe. The information confirms or adds to previously known facts of host relationship and may contribute to eventual understanding of detailed factors in the complex chain of disease transmission.

SUMMARY

To add to basic knowledge of rodent-borne diseases, a Field Station at Santa Fe, New Mexico, has investigated mammals and their ectoparasites.

Data, obtained primarily through repeated live-trapping in a semiarid area of the Upper Sonoran Life Zone, were supplemented with collections by

TABLE 2.—Most commonly collected mammals[1] and Fleas.

Hosts	*Fleas*
Sylvilagus audubonii	Hoplopsyllus affinis, Cediopsylla i. inaequalis
Cynomys gunnisoni	Opisocrostis hirsutus, O. tuberculatus cynomuris
Citellus spilosoma	Thrassis pansus
Citellus lateralis	Oropsylla idahoensis, Hoplopsyllus anomalus
Eutamias minimus	Monopsyllus eumolpi
Eutamias quadrivitattus	Monopsyllus eumolpi
Thomomys talpoides	Foxella ignota
Perognathus flavus	Meringis jamesoni
Dipodomys spectabilis	Meringis nidi, M. rectus
Dipodomys ordii	Meringis nidi, M. parkeri
Reithrodontomys megalotis	Orchopeas leucopus
Peromyscus maniculatus	Orchopeas leucopus, Monopsyllus wagneri
Peromyscus leucopus	Orchopeas leucopus, Monopsyllus wagneri
Peromyscus truei	Orchopeas leucopus, Monopsyllus wagneri
Peromyscus boylii	Orchopeas leucopus, Malaraeus sinomus, Monopsyllus wagneri
Peromyscus nasutus	Orchopeas leucopus, Monopsyllus wagneri
Onychomys leucogaster	Monopsyllus exilis
Neotoma micropus	Orchopeas sexdentatus
Neotoma albigula	Orchopeas sexdentatus
Microtus longicaudus	Peromyscopsylla hamifer vigens

[1] Species with less than 10 examinations are excluded.

break-back trapping in other locations which also included Transition and Canadian Life Zones.

From July 1951 to February 4, 1954, a total of 8,784 mammals of 34 species were examined. Over 26,000 fleas of 54 species were collected. For each species of mammal, observations are given on reproduction, local distribution, and general abundance of the most frequently collected species of fleas.

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Comparative Infestations by Ectoparasites of Two Native Rats of Sansapor, New Guinea

Carl O. Mohr[1]

Communicable Disease Center, Public Health Service, U. S. Department of Health, Education, and Welfare and Emory University Field Station, Newton, Georgia

While stationed at Sansapor on the west coast of New Guinea in 1944, the writer made a survey of the chiggers in various habitats in order to gain some information as to floral cover which might harbor the vector of scrub typhus (*Trombicula deliensis* Walch) and the inducers of scrub-itch (*T. hirsti* Samb., *T. wichmanni* Ouds., *Schöngastia schüffneri* Walch, and *S. vandersandei* Ouds.). Rats, easily caught in traps, were good collectors of larvae of those species which parasitized them and, being rather closely confined to given types of habitats, proved good aids to making the survey: The data pertaining to percentages of rats infested were published (Mohr, 1947). Data pertaining to the average number per infested host of two New Guinea species (the coarse-haired rat, *Rattus ruber jobiensis* and the Pacific-island rat, *R. exulans manoquareus,* fig. 1) are recorded in the present paper and compared to available data (Griffiths, 1947) on the Pacific island rat. Griffiths' data are reinterpreted for this purpose (table 1). Records from several other species of mammals are included.

Relatively few studies of the absolute numbers of these chiggers per host have been published and, although different species of rats usually have decidedly different populations of chiggers, data from different host-species frequently are mixed and the epizootiological significance thereby obscured. Philip, Traub, and Smadel (1949) recorded averages of from 50 to 270 per *Rattus exulans,* 48 through 380 per *R. argentiventer* and 64 per *R. whiteheadi* in Malaya during the months of April-July, 1948; Traub and Frick (1950) estimated the average number of vector mites *(T. akamushi* and *T. deliensis)* to vary from 12 to 550 per *Rattus r. argentiventer* in infectious areas at Selangor, Malaya, where the average depended on habitats from which the hosts were taken; and Traub, Newson, Walton and Audy (1954) reported averages of from 220 to 1200 per rat on *R. rattus* and *R. mulleri* in North Borneo. Aside from those provided by Griffiths, there are no specific population data from the New Guinea rats.

Procedures and Methods

Mammals for the present study were caught alive in box traps or pit-falls and in ordinary rat traps. In either case, they lost some ectoparasites from the moment caught, generally sometime between dusk and 9 a.m. The dead ones probably lost ectoparasites faster than the live ones and the rate of loss

[1] Present address: Illinois Natural History Survey, Urbana.

Fig. 1.—A. New Guinea coarse-haired rat; B. Pacific-islands rat. Both natural size.

undoubtedly varied considerably with the species of ectoparasite, facts which must be taken into account when comparing results of various studies.

The collections were made during the dry season from September 15 through December, 1944. The specimens for which population data are recorded were examined carefully for any ectoparasites with the exception of minute hair mites and mange mites. No examination was made of the nasal cavity, or of the deep external auditory canal which, according to Philip and Woodward (1946), is infested at Manila by *Ascöschongastia indica.* Any such infestations were therefore missed and the average number of this species recorded per host represents only the average in the ear conchae or on the body.

HOSTS AND ECTOPARASITES

The New Guinea coarse-haired rat, a species of about the size of the common rat *(Rattus norvegicus)* and the Pacific-islands rat, a small mouse-like species, were most numerous in the catch. A few other mammals were also caught.

PACIFIC-ISLANDS RAT, *Rattus exulans manoquarius.*—Selected specimens were identified by Tate (1951).

This small rat previously was recorded as *Rattus exulans* by the writer (1947); as *R. concolor manoquarius* by Griffiths (1947); and as *R. concolor browni* by Kohls et al. (1945) who worked in the same area ("E") at Sansapor, taking 16 during the period August 24-29.

Ectoparasites taken from 40 of these rats by the writer, 16 by Kohls et al., and an unstated number by Griffiths include the chiggers, *T. deliensis, S. vandersandei* (Syn. *S. blestowei* Gunth.), *S. schüffneri* (Syn. *S. pusilla*), *S. mohri, A. indica, Walchia disparunguis* Ouds. (Syn. *W. glabrum* Walch, and *W. pingue* of Griffiths (1947); the parasitid rat mites, *Laelaps nuttalli* Hirst (Syn. *L. hawaiiensis* Ewing) and *Cosmolaelaps* sp.; a nymphal tick, *Amblyomma* sp.; and the louse, *Hoplopleura oenomydis* Ferris (Syn. *H. pacifica* Ewing). Neither of two scrub-itch chiggers, *T. wichmanni* nor *T. hirsti* was found on rats although the former was reported present at Sansapor by Griffiths and the latter by Kohls et al., as *S. buloloensis.*

Only 7 rats of the 40 live specimens of this species reported by the writer (1947) bore *T. deliensis.* This is due in part to the fact that most of the rats were caught in cleared and relatively dry areas, and, in part, to the fact that they bear relatively few chiggers anyway. Fifteen of the 16 hosts examined by Kohls et al. (1945) yielded them. Of the 56 specimens examined by the writer, and Kohls et al., only about 40 percent bore *T. deliensis.*

An average of only 4.5 individuals of this species occurred on 31 Pacific-islands rats examined by Griffiths (1947) from uncleared native garden (table 1). Griffiths indicates that he captured several species of rats, one of them, *Rattus (ruber) ringens* and the other *Melomys* sp. but subsequent correspondence indicates that he caught only the Pacific-islands rat in this habitat. An average of 32 per rat occurred on 21 Pacific-islands rats (table 1) examined by the writer from uncleared native garden within the C Company area of Griffiths' fig. 1 (1947) and a 100 or more yards from the garden occupied

TABLE 1.—Ectoparasite and habitat data on Pacific-Islands rats modified from Griffiths (1947), with additional data by Mohr.

Habitat	Number of rats			Calculated avg. no. of each species per rat.							Percent of chiggers which were:						
	examined	with chiggers	Avg. no. chiggers per rat	T. deliensis	W. disparunguis	S. vandersandei	S. schüffneri	S. mohri	A. indica	N. oudemansi	Identified	T. deliensis	W. disparunguis	S. vandersandei	S. schüffneri	A. indica	N. oudemansi
Beach, uncleared	7*	7	72	63	2.4	0	0	0	5.8	0.6	20	38	3.3	0	0	8.1	0.8
Native garden, partially cleared	7**	7	32	20	0	0	9.6	0	0	2.1	41	63	0	0	30	0	6.5
Rain forest not near beach, uncleared (B)†	2**	2	45	19	26	0	0	0	0	0	85	43	57	0	0	0	0
Native garden, uncleared (D)	31**	26	21	4.5	11	4.1	0.4	0	0	0.8	27	28	49	18	1.5	0	3.4
Beach adjacent to grass, uncleared	5*	2	9.8	9.6	0	0.2	0	0	0	0	100	98	0	2	0	0	0
Summary	52	44	30	24	8	1	2	0	1	1	46	64	22	4	6	2	2
Mohr Data—Uncleared native garden (D) near rain forest (B)	21	12	52	32	17	2.3	0.4	0.2	0.1	0	19	62	33	4.4	0.8	0.2	0

*Probably pure collection of Pacific-Islands rats (R. exulans); the author does not recall whether or not other species occurred in these collections, but the habitat in question is one not ordinarily inhabited by other rats.

**Pure collection of Pacific-Islands rats.

†Letters indicate which areas were the same or essentially like those from which Mohr (1947) took coarse-haired rats.

by A and B companies and sampled by Griffiths and Kohls. Greatest number of individuals observed on a single Pacific-islands rat was about 430 on an individual caught in uncleared garden.

The Pacific-islands rat is credited by Harrison and Audy (1951) with being a primary host of *T. deliensis* in the New Guinea area and providing a distribution to this chigger far beyond the main body of its range which chiefly is in southern Asia where the white-breasted races of *Rattus rattus* are the primary reservoir. There is an abundance of evidence on this point; the Pacific-islands rat has been found where no other species of mammals could have been key host (Philip and Kohls, 1951), that is on an island where this rat and pigs, which bore few chiggers, were the only available mammalian hosts, and on which birds, though infested appeared to be of minor importance as food-furnishing hosts. Also in the Sansapor area, the Pacific-islands rat bore this chigger in habitats where other species appeared to be too scarce.

The scrub-itch chiggers, *S. vandersandei* and *S. schüffneri*, averaged 2.3 and 0.4 respectively on the 21 rats taken by the writer and 4.1 and 0.4 on the 31 by Griffiths. Kohls et al. reported several specimens of each from 8 of 16 of these rats. Separation of these was uncertain to the writer.

An average of 11 *W. disparunguis* occurred on the 31 taken by Griffiths and an average of 17 on the 21 taken by the writer. Three hundred fifty-three occurred on one Pacific-islands rat taken by the writer.

The rat-nest, chigger *A. indica*, occurred on only one of the 21 Pacific-islands rats examined by the writer and on none of the 31 by Griffiths or the 16 of those examined by Kohls et al. (1945). There were 3 on the infested rat.

This infestation of the Pacific-islands rat by the rat-nest chigger is of interest; it was found abundant by Wharton (1946), in Guam in the rain forest that tops the abrupt coral cliffs and also in the coconut groves but not on rodents living in grass-covered, unforested areas. The Pacific-islands rat, which is an inhabitant of primarily grassy areas on Guam as in the Sansapor area, was uniformly free of this chigger, whereas a larger rat, *Rattus mindanensis*, was commonly infested but only when living in the rain forest and coconut groves. The infested Pacific-islands rat which the writer found is from a light growth of scrub.

An average of 0.8 *N. oudemansi* occurred on 31 rats taken by Griffiths. Highest was 2 per rat. None occurred on the 21 taken by the writer. Four *S. mohri* (Womersley, 1952) occurred on one of the 21 and one also was present on a dead rat. (*S. mohri* is the species recorded by the writer (1947) as *Schöngastia* "n. sp. 1" from *Rattus exulans* on which it was associated with many *W. disparunguis* and a few *S. schüffneri*. The other species, recorded as "n. sp. 2", from the Philippine Islands in the same publication is *Ascoschöngastia philippensis* Philip and Woodward, 1946).

The 2 species of parasitid mites and nymphs of *Amblyomma* were found on several individuals. Seventeen *Laelaps nuttalli* were found on one specimen.

Only one of these rats taken by the writer bore the tick, there being only one individual. This is the rat which also bore the rat-nest chigger.

TABLE 2.—Ectoparasite and habitat data on coarse-haired rat.

Habitat	No. of rats examined	T. deliensis		W. disparunguis		S. vandersandei		S. schüffneri		A. indica		N. oudemansi		L. nuttalli		E. echidninus		Amblyomma		H. oenomydis	
		No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:	No. of rats with:	Avg. no. per rat infested by:
CLEARED																					
Now in short mixed vegetation (E, F, G)*	11	9	437	2	5	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
UNCLEARED																					
Rain forest and margin near "D"																					
Moist (A)	17	17	687	13	9	1	4	1	3	1	5	....	....	9	36	....	1	3	8	7	62
Dry (B)	11	11	282	....	....	....	....	....	....	2	12	....	....	....	....	....	....	1	1	....	....
Native garden:																					
Moist (D)	4	4	336	1	8	....	....	....	....	....	....	....	....	1	3	1	3	1	15	....	....
Dry (D)	8	7	173	....	....	....	....	1	10	....	....	3	12	3	4	....	....	....	....	....	....
SUMMARY	51	48	383	16	7	1	4	2	7	3	8	3	12	13	14	1	3	5	8	7	62
PERCENT OF TOTAL CHIGGERS	....	91	....	....	1.5	....	1.0	....	1.5	....	1.5	....	3	....	....	....	....	....	....	....	....

*Letters indicate the grouping of areas used in a previous report (Mohr, 1947).

Three of the hosts from which these ectoparasites were taken by the writer are in the American Museum of Natural History (AMNH) and several are in the United States National Museum (USNM). Representative ectoparasites are in the collection of the South Australian Museum, and the ticks and mite, *L. nuttalli*, are in the *collection of the USNM.*

COARSE-HAIRED RAT, *Rattus ruber jobiensis.*—This rat was recorded as *Rattus ringens* by the writer (1947) and as *Rattus ringens ratticolor* by Griffiths (1947). A recent revision by Tate (1951) based in part on specimens furnished him by the writer, makes it *Rattus ruber jobiensis.*

Fifty-one live rats of this species were examined for ectoparasites (table 2). Eleven dead rats also were examined. Those from moist rain forest, were captured either along wide basins of creeks which were dry at the season when this investigation was made, or in an extensive, low area in which the soil and humus were soggy or very moist, but without standing water and those from margin at the abrupt margins between jungle and garden. Those from dry rain forest were from higher relatively sandy areas. Those from moist and dry native garden were from similar areas in native garden except that there was no tall, heavy floral canopy over the garden.

These rats yielded the chiggers *T. deliensis, S. vandersandei, S. schüffneri, W. disparunguis, A. indica rattus* Wom., and *Neöschongastia oudemansi* (Syn. *N. impar* Gunther); the parasitid rat mites *Laelaps nuttalli, Echinolaelaps echidninus* Berl., and *Bdellonyssus bacoti* (Hirst); a nymphal tick, *Amblyomma* sp.; the louse *Hoplopleura oenomydis;* and one flea *Stivalius* sp. identified by Dr. Robert Traub. Between 30 and 50 percent of the chiggers on each rat were identified, the total number was counted and the number of each species was then calculated.

Most (48 of 51) live coarse-haired rats bore *T. deliensis.* Sixteen bore *W. disparunguis.*

Only one, two, or three bore the rat-nest chigger *A. indica;* the scrub-itch chiggers *S. vandersandei* and *S. schüffneri;* and *N. oudemansi.*

Thirteen bore the mite, *L. nuttalli,* and five bore the nymphal ticks, Amblyomma sp. Only one rat of the 51 bore the flea.

T. deliensis occurred most abundantly on coarse-haired rats from uncleared rain forest (687 per infested rat), and least so on the few taken in dry native garden (173 per infested rat). Over 4000 were taken from one individual from moist uncleared forest (Mohr, 1947).

W. disparunguis averaged 9 per infested rat. Greatest infestation per single rat was one of 44. The infestation therefore did not vary decidedly from those on the Pacific-islands rats. The rat-nest chigger *A. indica* averaged up to 12, or larger than that on the Pacific-islands rat. There were 21 on one rat. *N. oudemansi* averaged 12. The scrub-itch chiggers, *S. vandersandei* and *S. schüffneri* averaged 4 and 7. *S. schüffneri* apparently infests habitats of coarse-haired rats in fairly large numbers.

Of the total of 62 rats, 51 alive and 11 dead, *T. deliensis* occurred alone on 27, on 17 of these rats with *W. disparunguis,* on 7 with *Amblyomma* sp.,

on 5 with *S. schüffneri,* on 6 with *N. oudemansi,* on 4 with *S. vandersandei,* and on 3 with *A. indica.*

W. disparunguis occurred with *S. schüffneri* on 4, with *A. indica* on 2, and on 2 each with *S. vandersandei, N. oudemansi* and the tick.

A. indica was not found on the same host individual with *S. schüffneri, N. oudemansi* or *S. vandersandei* or the tick. *S. vandersandei* was not found on the same host with *A. indica, N. oudemansi* or the tick. *S. schüffneri* and *S. vandersandei* occurred together on 3 hosts.

Two species of parasitid mites, *L. nuttalli* and *E. echidninus,* one tick, *Amblyomma* sp. and a species of louse, *H. oenomydis* also were found. Although no rats from cleared areas bore them, it is not certain that that habitat was the most important factor except in the case of the tick; most of the rats taken in cleared habitats were taken a month or so later than were rats in uncleared areas. The difference may therefore be due to habitat, season, or chances in sampling.

Tick-infested rats bore an average of 15 ticks and regularly were heavily infested by *T. deliensis,* indicating joint occupancy of the more moist habitats.

Nine of the hosts from which these ectoparasites were taken are in the AMNH and a small number in the USNM. Those in the latter museum were identified by Dr. Remington Kellogg as *Rattus ringens coenorum.* Representative ticks, and mites, *E. echidninus, L. hawaiiensis,* and *B. bacoti,* and lice, *H. oenomydis (pacifica),* are in the USNM. Specimens of *N. oudemansi* are in the collection of the Rocky Mountain laboratory.

The coarse-haired rat is commonly infested by scrotal nematodes tentatively identified as members of the family Filarioidea by members of the Bureau of Animal Industry, Zoological Division, U. S. Department of Agricultural Research Center. Some immature specimens are in the USNM.

MOSAIC-TAILED UROMYS RAT, *Uromys* sp.—Two specimens were taken dead in traps and two specimens were taken alive.

The live specimens, from a dense stand of jungle with high undergrowth, bore *T. deliensis, W. disparunguis,* and *Amblyomma* sp. Both rats had fossae of both ears filled with chiggers and both bore between 100 and 200 chiggers. One *Uromys* bore 14 nymphs of the tick. The other bore only one. Abdominal nematodes were present in both, apparently the same species found in *Rattus ruber.*

The two hosts from which ectoparasites were taken are in the collection of the AMNH.

MARSUPIAL BANDICOOT, *Echymiptera doreyana* Q. & G. (identified by Remington Kellogg in 1944). One male bandicoot was examined immediately after being killed and is now in the collection of the USNM.

This animal bore 83 *T. deliensis,* 19 *S. schüffneri,* and 6 *S. mohri* on its abdomen, and 6 nymphs of a tick, *Amblyomma* sp., on its rump. One bandicoot of this species collected dead at Sansapor in 1945 by W. D. Fitzwater bore three *Schöngastia crinita* (Womersley, 1952).

Comparison of the Rats as Hosts

In general, the ability of a host species to support great numbers of a given ectoparasite, as well as for a high percentage of that host to be infested, is indicative of its excellence as a host. However, in the case of part-time parasites such as chiggers, host excellence is not necessarily disclosed by difference in the degree of infestation; the heavier infestation of coarse-haired rat by certain ectoparasites as compared to those of Pacific-islands rat could be the result of the following characteristics: 1) actual preference of the ectoparasite; 2) structure or physiology of the host which may cause it to be particularly susceptible to infestation; 3) lack of ability to cleanse itself of the chiggers; 4) greater size, permitting a greater number of chiggers to find space on it; 5) tendency to spend a greater share of its time in the habitat in which the parasite is most abundant; 6) digging, foraging, resting, or other habits which expose it more to ectoparasites; 7) relatively small numbers in chigger-infested habitats, making this less numerous host-species more subject to individual attack than the more numerous Pacific-islands rat; 8) tendency of the individual rats to cover a wide territory during daily activity, hence to be exposed to more chiggers.

Probably factors 1, 2, and 3 had little to do with the larger infestation of the coarse-haired rat as compared with the Pacific-islands rat but the others are characteristics of the larger species which favor larger infestation by *T. deliensis*. There appears to be more extensive, tender space in their ears. At least during the dry season in the Sansapor area, the coarse-haired rat occurred most commonly in the tree-shrub habitats which yielded the greater number of chiggers regardless of host; a gradient showing the relationship of its abundance to height and density of floral cover as revealed by the use of snap rat-traps, indicates that coarse-haired rats are found practically to the exclusion of Pacific-islands rats in the heavily forested and dense-shrub habitats (Mohr, 1947) but that the absolute and relative number of Pacific-islands rats is greatest in the thinner shrub and herb habitats from which Kohls et al. (1945) obtained only Pacific-islands rats.

That the habitats (uncleared rain forest and margin, and moist native garden) in which the coarse-haired rat spends the greater share of its time were more suitable to *T. deliensis* than were the drier, shrub-herb habitats, is indicated by the fact that the Pacific-islands rat, as well as the coarse-haired rat, gathered more *T. deliensis* onto itself in the denser habitats than in the others; about 80 per infested rat in shrubby uncleared native garden near rain forest and 6.4 per rat from dry native garden. That this differential is consistent is indicated by Blake et al. (1945); who state, of related rats, "heavier infestations were encountered on *R. mordax*, *R. praetor* (?), and on *R. gestri* than on *R. concolor browni* in the same specific locations in the bush."

Although no data specific to the daily range of activity of either of these rats in New Guinea is available, it is probable that the larger rat also has the larger average daily range; this is a commonly-recognized principle for species of similar food habits.

SUMMARY AND CONCLUSIONS

Infestations by chiggers (*Trombicula deliensis* Walch, *Schöngastia schüffneri* Walch, *S. vandersandei* Oudemans, *S. mohri* Womersley, *Walchia disparunguis* Oudemans, *Aschochöngastia indica rattus* Womersley, *Neoschöngastia oudemansi* Walch), of two species of rats (*Rattus exulans manoquarius* Sody and *Rattus ruber jobiensis* Rummler) are compared for Sansapor, New Guinea for the dry period, August-December 1944.

T. deliensis was the more numerous on *R. r. jobiensis*. An average of 687 occurred on this rat in the habitat apparently most favorable during the dry season. An average of only 63 was found on *R. e. manoquarius* in the habitat in which it was most heavily infested. The scrub-itch chiggers *S. schüffneri* and *S. vandersandei* apparently are the more common in habitats occupied by *Rattus ruber*.

Habitat selection by these two species of rats is such that, although there is some overlap of range and population, the combined area covered by the two key hosts is greater than that occupied by either one alone, thus makes available to certain of the chiggers, particularly *T. deliensis*, a greater amount of area and a greater gradient of microclimatic conditions than one species of rat alone could offer. Infestations on *Rattus ruber* are among the highest recorded for rats.

Related species of rats and a marsupial bandicoot were caught in small numbers in the same habitats. The bandicoot evidently is an additional, essential or neo-essential host in the area.

Several other species of ectoparasites were taken: *Laelaps nuttalli* Hirst; *Echinolaelaps echnidninus* Berl.; *Hoplopleura oenomydis* Ferris; *Amblyomma* sp.; and *Stivalius* sp.

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Kinds and Distribution of Wild Rodents and Their Ectoparasites in Egypt[1,2]

M. S. Briscoe[3]
Howard University, Washington, D. C.

The writer made a survey in Egypt during the months of July, August, September, and part of October, 1953, to determine the kinds and distribution of wild rodents and the ectoparasites that they harbor, and to provide some preliminary data on relationship to temperature, humidity, soil and vegetation types. Results of this survey are reported in this paper.

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Regional Geography

Egypt is situated between the parallels of 22° and 32° North latitude. Except for the Nile River Valley the country is barren desert. In Upper Egypt the Nile River Valley is narrow, in Lower Egypt the valley widens as a low-lying deltaic plain.

[1] The Office of Naval Research, Biology Branch, Department of the Navy, sent the writer to Egypt during the summer of 1953 to investigate the distribution of wild rodents and their ectoparasites and to tabulate data on relationship to climate, soil and vegetation types. These studies were undertaken as part of the investigations on potential or known arthropod vectors of disease in Egypt and their rodent hosts under the direction of Harry H. Hoogstraal, Head, Dept. of Medical Zoology, U. S. Naval Medical Research Unit, No. 3, Cairo, Egypt.

[2] These studies were aided by a contract between the Office of Naval Research, Department of the Navy, and Howard University, NR 160-233.

[3] The opinions or assertions contained herein are the private ones of the writer and are not to be construed as official or reflecting the views of the Navy Department or the naval service at large.

The Nile Valley is a rift valley formed by the settling of a narrow belt in the neighborhood of a line of fracture on the earth's surface. West of this valley the Western Desert extends to the Libyan border. The Eastern Desert, on the other hand, stretches from this valley to the Red Sea and the Palestine boundary. The portion of the Western Desert along the Mediterranean Sea is called the coastal desert. The low-lying areas, the Faiyum and the Wadi Natroun, in the Western Desert constitute low-lying saline deserts (fig. 1). For the most part the Eastern and Western Deserts consist of outcroppings of granite and gravelly limestone plateaus. To a lesser extent they contain some stretches with sand hills. South of Cairo the deserts rise to an elevation of 1,000 to 1,500 feet above sea level in a series of terraces intersected by ravines.

More detailed descriptions of these regions are given under the heading of *Distribution of the Rodents* where interrelationships are indicated.

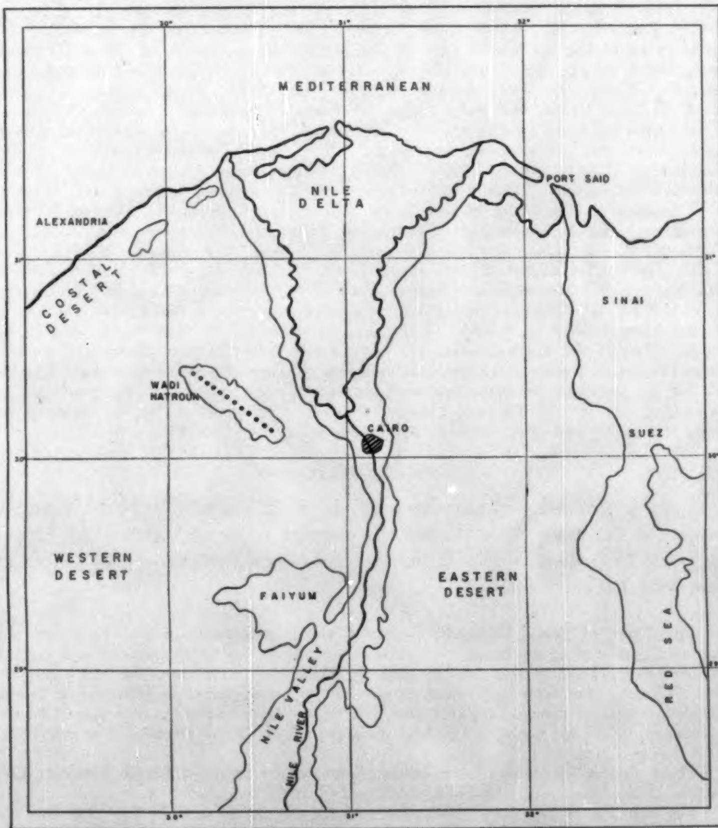

Fig. 1.—Areas in Egypt where collections were made.

CLIMATE

The summer in Egypt is dry and hot, the winter is moister and cooler, the conditions being somewhat more extreme in the desert areas than in the Nile Valley. The annual mean temperature in the Nile Valley is 70° F with monthly means ranging from 56° F in January to 82° F in July. The same annual mean obtains in the low-lying saline desert with the lowest monthly mean 53° F in January and 83° in July and August. The mean annual total precipitation is 22 mm in the former, 17 mm in the latter, with no rain in either region during the period from June to September inclusive. The mean annual relative humidity is 75 percent in the Nile Valley and 58 percent in the low-lying saline deserts.

METHODS

The specimens of rodents in 9 species collected during this survey were captured in their burrows. They were put in separate muslin bags and then placed in glass jars and killed with chloroform. Before they were removed from their burrows, however, temperature and relative humidity readings were taken outside and inside of the burrows with a portable Aminco-Dunmore electric hygrometer.

DISTRIBUTION OF THE RODENTS

Throughout this study attention has been focused primarily on wild rodents and their ectoparasites in the cutlivated Nile Valley and various parts of the barren deserts (fig. 1). The most recent names of the rodents (listed below) have been validated according to Ellerman and Morrison-Scott (1951).

CRICETIDAE

Gerbillus pyramidum Geoffroy (Greater Egyptian Gerbil). Range: Egypt and Algeria.

G. gerbillus Olivier (Lesser Egyptian Gerbil). Range: Egypt, Libya, Algeria to Palestine.

Psammomys obesus Cretzschmar (Fat Sand Rat). Range: Algeria, Tunis, Eastwards into Arabia and Palestine.

Meriones shawi Duverney (Shaw's Jird). Range: Morocco, Algeria, Tunis, Libya, Egypt, Palestine.

M. crassus Sundevall (Sundevall's Jird). Range: Sinai, Arabia, Egypt, Sudan, Algeria.

MURIDAE

Arvicanthis niloticus Desmarest (Kusu Rat). Range: Egypt.

Nesokia indica Gray and Hardwicke (Bandicoot Rat). Range: Egypt, South Waziristan, Punjab, Sind, Delhi and Fategarh in the United Provinces, Rajputana, Kumaon, Iraq, Kabul in Afghanistan.

DIPODIDAE

Jaculus orientalis Erxleben (Greater Egyptian Jerboa). Range: Egypt, Libya, Tunis, Algeria.

J. jaculus Linnaeus (Lesser Egyptian Jerboa). Range: Egypt. The typical race has also been reported from Palestine.

CULTIVATED NILE VALLEY

The kusu rat, *Arvicanthis* niloticus, is restricted to the cultivated Nile Valley (fig. 1). Its burrows were found in various habitats throughout this densely inhabited area. Some were constructed on the side of steep banks of hard sun-dried alluvial mud near irrigation canals. Many of these banks were thickly populated with *Eragrostis cynosuriodes* (Retz.) Roem. et Schult. The grassy covering of other banks usually consisted of *Phragmites communis* Trin. This grass also formed a low bushy covering in fallow areas and fair stands in brackish water. The most profuse growth observed, however, was on canal banks. Some banks were sparsely fringed with *Ricinus communis L.*

In native villages the burrows of *Arvicanthis niloticus* were constructed for the most part at the base of date palms. On one occasion 7 of these kusu rats were captured in a burrow beneath a pile of limestone rocks on a flat barren area adjacent to an irrigated cotton field.

Burrows of *Arvicanthis niloticus* ranged in length from 3 to 10 feet and from 1 to 2½ feet in depth. Those near irrigation canals had a relative humidity ranging from 54 to 78 percent and temperatures from 68° to 94° F (August 1953). Humidity ranges outside of these burrows (44 to 66 percent) were lower than those measured within; the outside temperatures were higher (90° to 106° F).

The humidities in the burrows at the base of date palms were high during the early morning hours but decreased towards noon. The inside temperatures showed a gradual increase from 8:30 A. M. to 11:30 A. M. but dropped 2 degrees at 1 P. M. Temperatures outside the burrows were consistently higher than those within the burrows while the outside humidities were correspondingly lower.

The temperature of the burrow constructed beneath the limestone rocks was 84° F, the relative humidity 66 percent. Temperature of the air outside was 90° F, the relative humidity 56.5 percent (5 August 1953 at 9:20 A. M.).

In areas of the cultivated Nile Valley where flat alluvial strips are covered with wind-blown sand, vegetational types gradually change into desert conditions. Plants indicating transitions in conditions from the cultivated Nile Valley to desert are: *Calligonum comosum* L'Herit, *Stipa tortilis* Asch., and *Tamarix arborea* Bunge.

Habitats of the other rodents were found in various parts of the Eastern and Western Deserts (fig. 1). The Eastern Desert is strikingly different from the Western Desert in its relief, vegetation, and geology (Davis, 1953). In certain places the Eastern Desert is dissected by wadis. After intervals of several years these wadis are subject to sporadic torrents that may destroy the vegetation and wash away the soil (Kassas, 1952). This may explain the rather complex pattern of the plant cover in these habitats. Important species were *Zilla spinosa* (Forsk.) Prantl, *Panicum turgidum* Forsk., *Farsetia aegyptiaca* Turra Farset, and *Heliotropium luteum* Poir. Water tends to fill the wadis for short periods only after very heavy rainfall in the mountains. Ten millimeters of rain is enough to cause flooding (Davis, 1953).

The Western Desert (fig. 1) consists chiefly of barren gravelly plains upon which may be seen occasional barren sand hills. The area is devoid of

vegetation where wide expanses of gravel occur. The highest air temperature recorded in the barren regions of the Western Desert for July was 120° F at 10:30 A. M., 22 July 1953. The lowest temperature was 68° F at 7:30 A. M., 30 July 1953. The highest relative humidity measured in the atmosphere was 54 percent at 8:30 A. M., 29 July 1953 and the lowest, 16.8 percent at 12:30 P. M., 31 July 1953. The highest burrow temperature recorded was 108° F at noon 17 July 1953 in a burrow occupied by *Gerbillus gerbillus* and 108° F at 12:30 P. M., 31 July 1953 in a burrow inhabited by *G. pyramidum*. The highest relative humidity (75.5 percent) was measured at 9:00 A. M., 29 July 1953 in a burrow inhabited by *G. pyramidum*. The lowest relative humidity (25.5 percent) was recorded at noon 17 July 1953 in a burrow inhabited by *G. gerbillus*. It can be seen that a desert rodent would pass through quite a range of climatological conditions if it entered or left its burrow during the day. For example, on 27 July 1953 at 10:45 A. M., the air temperature on the barren areas of the deserts was 102° F; ground temperature, 115° F; and the burrow temperature, 90° F. During this period the relative humidity of the atmosphere was 34 percent; at ground level, 33.5 percent; and the burrow, 55 percent. At 11:20 A. M. on the same day the air temperature was 100° F; the ground temperature, 120° F; and the burrow temperature, 98° F. During this same period the relative humidity of the atmosphere was 35 percent; at ground level, 31.5 percent; and the burrow, 46.5 percent.

At any given time variations in temperature and relative humidity could be recorded in closely adjacent places. The effect of these variations on the activity of the tenebrionid beetle, *Prionotheca coronata* Ol., attracted our attention. These insects, commonly seen on the surface in the barren regions of the deserts, would cease their activities during the hottest part of the day and either dig into the sand or enter small burrows previously constructed. The reactions of these insects indicated that temperature and relative humidity also played an important part in controlling their diurnal activities.

Burrows constructed by *Gerbillus gerbillus* and *G. pyramidium* were somewhat similar in structure although the two species were never found together. These burrows ranged from 3 to 12 feet in length and from 1 to 3½ feet in depth; some were fairly straight and others were slightly curved or U-shaped. All of them had their entrances plugged with sand.

The majority of the burrows of *Gerbillus gerbillus* were found at the base of hillocks formed by wind-blown sand. These hillocks were held in place by two species of grasses, *Aristida scoparia* and *Panicum turgidum*, that appeared to be good sand-binders. These grasses are characteristic of the sandy plains. A few of the burrows were located on the side of shallow sand-filled wadis; some were also constructed on flat sandy plains on which occurred sparse tufts of *Panicum turgidum* and *Heliotropium luteum*. Only a small number of burrows made by *Gerbillus pyramidum* were located. They were found in areas similar to those of *G. gerbillus*. Sandy places inhabited by these two gerbils furnished a loose substratum in which burrows could be easily dug.

Plugged burrows of *Jaculus jaculus* were constructed in the hard clayey-sand

slopes in barren areas of the deserts. These slopes descended gradually as much as 250 feet and were devoid of vegetation. Ground temperatures on these barren declivities ranged from 78° to 104° F during the first two weeks in September, 1953, when they were examined for rodent burrows. Atmospheric humidity ranged from 33.5 to 48 percent. Within the burrows the temperatures varied from 80° to 100° F and the relative humidity ranged from 35.5 to 49.5 percent. The depth of some of these burrows was much greater than those of any other species of rodents investigated in this survey. They extended from 1 to 5½ feet below the surface and were 2 to 13 feet long. Considerable time was utilized digging at great depths in this hard soil.

Entrances to burrows made by *Meriones crassus* remained opened. Usually there were several emergency exits which the rodent invariably used in its attempt to escape as the diggers removed soil from the corridors. These well-ventilated burrows varied in length from 3 to 15 feet and a depth from 1 to 3½ feet. During the last week in September, 1953, burrow temperatures ranged from 77° to 97° F and their relative humidity from 24 to 78 percent. Air temperatures during this period varied from 78° to 103° F; the relative humidity from 21.5 to 77 percent.

Many burrows of *Meriones crassus* were found on the sides of shallow sand-filled wadis in the vicinity of the Cairo-Suez road. The edges of these wadis were fringed with bushes of *Lasiurus hirsutus*. Hard clayey-sand banks along the Cairo-Suez road were perforated with the open burrows of this rodent and bordered with bushes of *Haloxylon salicornicum*. In areas formerly occupied by army barracks this rodent had constructed its burrows in the hard clayey-sand beneath empty tins of various sizes and beneath broken bottles and old automobile tires. A sparse growth of *Panicum turgidum* had established itself in the midst of this detritus.

The present land surfaces of the coastal portion of the Western Desert consist chiefly of oolitic limestone (Ball 1939). The coastal region under observation during this survey comprises the area around Burg-el-Arab in the Mariut district about 25 miles west of Alexandria (fig. 1). A ridge of oolitic limestone parallels this part of the coastline for long distances. Another ridge, at a distance inland, runs parallel with that on the coast. A belt of white sand, together with sand hills of various sizes, also extends along the shore. Small white hillocks of wind-blown sand that fringed the shore-line supported communities of *Calamagrostis arenaria* (L.) and *Pancratium maritimum* L.

The area between the coastal and inland ridges of limestone is interrupted by sandy depressions that form salt marshes with characteristic halophytic communities. Typical marginal plants of these saline lagoons are *Suaeda fruticosa* Forsk., and *Salicornia fruticosa* (L.). The absence of halophytes in the central part of these salt beds is due to excessive accumulation of salt (Tadros, 1953).

A semi-desert lying near the marshes was dotted with hillocks and carpeted with perennial shrubs, *Limoniastrum monopetalum* Boiss. and *Arthrocnemum glaucum* (Del.) Unger-Sternb. Open burrows of *Psammomys obesus* were found at the base of these hillocks in the flat loamy soil. These burrows ranged from 8 to 12 feet in length and from 1 to 2 feet in depth. Some of

them presented 3 to 5 entrances and were provided with an assemblage of lateral corridors. During the middle of August, 1953, when these rodents were captured, the temperature in their burrows varied from 80° to 92° F while the relative humidity varied from 36.5 to 53.5 percent.

Plugged burrows of *Jaculus orientalis* and open burrows of *Meriones shawi* were located on barren isolated sand slopes approximately 5 miles from the Mediterranean Sea. Intervening sand flats were heavily furrowed and covered with fragments of limestone. The burrows of *Jaculus orientalis* were 5 to 10 feet long and 2½ to 3 feet deep. Their temperatures ranged from 82° to 94° F; their relative humidity varied from 43 to 72 percent. Air temperatures during this period fluctuated between 86° and 96° F; the relative humidity from 36 to 59 percent.

Only two burrows of *Meriones shawi* were found. They were 10 feet long and 2½ feet deep. On 14 August 1953 when one of these rodents was captured the burrow temperature was 88° F and the relative humidity, 42 percent. The following day the temperature in a burrow inhabited by another specimen of *Meriones shawi* was 90° F and the relative humidity, 58.5 percent at 3:00 P. M. The air temperature was 94° F, the relative humidity, 39.5 percent.

Because of its proximity to the Mediterranean Sea the coastal area of the Western Desert receives more rain than any other part of Egypt. Most of the rain occurs during the winter months. The humidities in this area cause a great amount of dew precipitation which probably has an important influence on increasing the moisture content of the soil. This dew is of great importance in the water economy of perennials and summer annuals. It is perhaps the most obvious source of water for many small mammals though a more constant source is the vegetation (Buxton, 1923). From the point of view of climate the coastal region is more Mediterranean than anything else.

The Faiyum, a low-lying saline area in the Western Desert is about 50 miles southwest of Cairo (fig. 1). It lies from 100 to 250 feet below sea level. The lowest part of this region is occupied by a brackish lake—Birket Quarum—whose axis extends 25 miles and whose breadth is 5 miles at the widest point. Lacustrine deposits and rich alluvial soil in the Faiyum depression were laid down in Pleistocene and Recent geological periods (Ball, 1939). The soil layers are rich in chlorides and sulphates which are brought to or near the surface by the action of infiltrating water coming from high-level irrigation canals. Only a small amount of sand is mixed with this soil.

Plugged, damp burrows of the bandicoot rat, *Nesokia indica,* were constructed along the banks of the irrigation canals that intersected the surrounding terrain. *Alhagi maurorum* Medic., a thorny, deep rooted, much branched spinose shrub grows here in pure dense stands; it is an indicator of saline soils.

The burrows of the bandicoot rat were long, varying from 8 to 30 feet. Their depth ranged from 1½ to 2 feet. The corridors were a complicated labyrinthine network honey-combed with pockets. During the last week in August, 1953, the humidity in most of these damp burrows was high, ranging from 54.5 to 75 percent. A few, however, varied from 43 to 53 percent. Burrow temperatures fluctuated between 84° to 104° F. Air temperatures

ranged from 86° to 106° F while the humidity varied from 29.5 to 47 percent.

The valley of the Wadi Natroun, another low-lying saline region in the Western Desert, represents a new distributional record for *Nesokia indica*. This valley, 50 miles northwest of Cairo, is approximately 20 miles long and nowhere more than 5 miles wide (fig. 1). There is a chain of 12 small lakes in the valley which contain natural deposits of carbonate of soda and varying quantities of sodium chloride. The surface sand for some distance around the lakes is highly saline. The layer of clay beneath this sandy surface is also strongly impregnated with sodium chloride.

Stands of *Alhagi maurorum* were growing here as were similar species in the Faiyum. Burrows of the bandicoot rat were similar in structure to those examined in the Faiyum but were not as damp. Climatological readings taken in them during the first week in October, 1953, showed that their temperatures varied from 96° to 98° F and their relative humidity from 49 to 50 percent. Air temperatures during this period ranged from 98° to 101° F and and the relative humidity from 44 to 48 percent.

ECTOPARASITES

A total of 178 rodents (including 9 species) was collected during this study. Of this number 90 (50.5 percent) harbored ectoparasites; 88 or 49.4 percent were not parasitized. The total number of parasites collected from the rodent hosts was 1149. This number included 146 ticks; 365 fleas; 252 mites; and 386 lice. The average number of parasites per rat, however, is indicated by the parasite index in the following data.

	Number with ectoparasites	Number of ectoparasites	Parasite index
Arvicanthis niloticus	20	516	25.5
Gerbillus gerbillus	25	197	7.8
G. pyramidum	7	65	9.2
Jaculus jaculus	11	74	6.7
Meriones crassus	16	240	15.0
Jaculus orientalis	3	19	6.3
Meriones shawi	2	12	6.0
Psammomys obesus	1	2	2.0
Nesokia indica	5	15	3.0

TICKS

A total of 116 specimens of *Hyalomma* sp. (46 larvae; 46 nymphs; 10♂♂; 14♀♀ (table 1) was recovered from 20 rodents. There were 111 or 95.6 percent which were obtained from the barren regions of the deserts. Of this number (111) 47 or 40 percent were recovered from 9 specimens of *Gerbillus gerbillus;* 33 or 28.4 percent from 3 specimens of *G. pyramidum;* 14 or 12 percent from 5 specimens of *Jaculus jaculus;* and 17 or 14.6 percent from 1 specimen of *Meriones crassus*. From the coastal area of the Western Desert 3 or 2.5 percent of these ticks were obtained from 1 specimen of *Meriones shawi* and 2 or 1.7 percent from 1 specimen of the fat sand rat, *Psammomys obesus*. The majority of these ticks (80) were found on 9 specimens of *Gerbillus gerbillus* and 3 specimens of *G. pyramidum*. The largest

number found on a single host, 17, was recovered from host No. 184, *Meriones crassus* (13 larvae; 4 nymphs). A total of 18 specimens of *Hyalomma dromedarii* Koch (13 larvae; 4 nymphs; 1♂) was removed from 6 rodents. Most of these ticks, 15 or 83 percent, were found in the Wadi Natroun on the bandicoot rat, *Nesokia indica;* 3 or 17 percent were recovered from a single jird, *Meriones crassus,* in barren desert regions. In portions of the barren deserts 2 larvae of *Rhipicephalus* sp. were found on *Gerbillus pyramidum.* In the cultivated Nile Valley 3 nymphs of *Hyalomma leachii* (Aud.) were obtained from the kusu rat, *Arvicanthis niloticus.* A total of 7 specimens of *Ornithodorus erraticus* Lucas was found on 2 other kusu rats (1 host had 4 larvae and the other host had 3 nymphs).

FLEAS

A total of 139 specimens of *Xenopsylla cheopis* (Roths.) (73♂♂ and 63♀♀) was recovered from 21 rodents (table 1). Most of the fleas (93 or

TABLE 1.—Kinds and number of ticks and fleas collected on 9 species of rodents.

Hosts	No. of ticks collected	Hyalomma sp.	Ornithodorus erraticus	Rhipicephalus sp.	Haemaphysalis leachii	Hyalomma dromedarii
Arvicanthis niloticus	10	0	7	0	3	0
Gerbillus gerbillus	47	47	0	0	0	0
G. pyramidum	35	33	0	2	0	0
Jaculus jaculus	14	14	0	0	0	0
Meriones crassus	20	17	0	0	0	3
Jaculus orientalis	0	0	0	0	0	0
Meriones shawi	3	3	0	0	0	0
Psammomys obesus	2	2	0	0	0	0
Nesokia indica	15	0	0	0	0	15
Total	146	116	7	2	3	18

Hosts	No. of fleas collected	Ctenocephalides felis strongylus	Echidnophaga gallinacea	Mesopsylla tuschkan n. sp.	Synosternus cleopatrae	Synosternus pallidus	Xenopsylla cheopis	Xenopsylla conformis mycerini
Arvicanthis niloticus	99	0	6	0	0	0	93	0
Gerbillus gerbillus	39	2	0	0	36	0	1	0
G. pyramidum	11	0	0	0	11	0	0	0
Jaculus jaculus	37	0	0	0	1	0	36	0
Meriones crassus	169	0	0	0	20	15	9	125
Jaculus orientalis	7	0	0	7	0	0	0	0
Meriones shawi	3	0	0	0	3	0	0	0
Psammomys obesus	0	0	0	0	0	0	0	0
Nesokia indica	0	0	0	0	0	0	0	0
Total	365	2	6	7	71	15	139	125

66.1 percent) were taken from rodents in barren places of the deserts. The majority of them (93 or 66.1 percent) were recovered from 9 specimens of *Arvicanthis niloticus* in the cultivated Nile Valley. In barren sandy areas 36 or 25.8 percent were taken from 7 specimens of *Jaculus jaculus;* 9 or 6.5 percent from 4 specimens of *Meriones crassus;* and 1 was from *Gerbillus gerbillus.* A total of 125 specimens of *Xenopsylla conformis mycerini* (Roths.) (49♂♂ and 76♀♀) was obtained from 9 specimens of *Meriones crassus* in barren regions of the deserts. These fleas were not found on any of the other rodent hosts nor were they taken in any of the other areas investigated. The largest number of these ectoparasites on a single host was 33 (9♂♂ and 24♀♀); 2 males, on the other hand, represented the smallest number from one host. There were 71 specimens of *Synosternus cleopatrae* (Roths.) (43♂♂ and 28♀♀) which were recovered from 18 rodents. A total of 68 or 95.6 percent was found on rodents in barren desert areas. From these areas 36 of these fleas (50 percent) were recovered from 8 specimens of *Gerbillus gerbillus;* 11 or 15.5 percent from 2 specimens of *Gerbillus pyramidum;* 20 or 28.1 percent from 6 specimens of *Meriones crassus;* and 1 or 1.4 percent from 1 specimen of *Jaculus jaculus.* Only 3 or 4.2 percent were found on 1 specimen of *Meriones shawi* in the coastal region of the Western Desert. The predominant hosts harboring *Synosternus cleopatrae* were *Gerbillus gerbillus* (8 specimens) and *Meriones crassus* (6 specimens). Only 15 specimens of *Synosternus pallidus* (Tasch.) were found (2♂♂ and 13♀♀). They were taken from 4 jirds, *Meriones crassus,* in the barren parts of the desert. A total of 6 specimens of *Echidnophaga gallinacea* (West.) (3♂♂ and 3♀♀) was recovered from 2 kusu rats, *Arvicanthis niloticus,* in the cultivated Nile Valley. One of these rodents harbored 3♂♂; the other one had 3♀♀. The coastal region of the Western Desert yielded 7 specimens (4♂♂ and 3♀♀) of *Mesopysylla tuschkan* n. sp. They were recovered from a single jerboa, *Jaculus orientalis.* These fleas were not found in any of the other areas under investigation. Only 2 specimens of *Ctenocephalides felis strongylus* (Jordan) were found. Both of them were females and were recovered from one host, *Gerbillus gerbillus,* in barren desert areas.

MITES

A total of 252 mites was recovered from 7 species of rodents (table 2). Of this number 94 specimens of *Bdellonyssus bacoti* (Hirst) (22♂♂ and 72 nymphs) were collected from 15 rodent hosts. A total of 50 or 53.1 percent of these mites was found on 6 rodents in the cultivated Nile Valley; 18 or 19.1 percent were taken from 4 rodents in the coastal region of the Western Desert; and 26 or 27.6 percent were taken from 5 rodents in barren areas of the deserts. From barren desert areas 4 or 4.2 percent of *Bdellonyssus bacoti* were recovered from 1 specimen of *Gerbillus pyramidum;* 17 or 18 percent from 2 specimens of *G. gerbillus;* and 5 or 5.3 percent from *Jaculus jaculus.* In the cultivated Nile Valley a total of 50 or 53.1 percent of these mites was obtained from 6 specimens of *Arvicanthis niloticus.* From the coastal region of the Western Desert 6 or 6.3 percent of *Bdellonyssus bacoti* were found on the jird, *Meriones shawi* and 12 or 12.7 percent were obtained from the jerboa, *Jaculus orientalis.* Host No. 60, *Arvicanthis niloticus,* was

parasitized by 20 of these mites (3♀♀ and 17 nymphs); host No. 148, also a kusu rat, harbored 21 (3♀♀ and 18 nymphs). Approximately three times as many nymphs as female mites were present on the 15 rodent hosts (22♀♀; 72 nymphs). No males were found. A total of 102 mites representing new genera and species was found on 4 species of rodents. Of this number 82 *Ng. A, N. sp. D* were recovered from 15 rodents in barren portions of the deserts. There were 19 or 23.1 percent of these mites which were removed from 5 specimens of *Gerbillus gerbillus;* 3 or 3.6 percent from 2 specimens of *Gerbillus pyramidum;* 1 or 1.2 percent from 1 specimen of *Jaculus jaculus;* and 59 or 71.9 percent from 7 specimens of *Meriones crassus.* Host No. 92, *Meriones crassus,* harbored 19 of these ectoparasites (7♀♀ and 12 nymphs); host No. 182, also a specimen of *Meriones crassus,* had 18 (6♀♀ and 12 nymphs). Only 1 male was found. The number of nymphs obtained, 47, was much greater than that of the adults (1♂ and 34♀♀). There were 14 other mites (2♂♂; 8♀♀; 4 nymphs) collected in the barren regions of the deserts that also represented new genera and species (*Ng. A, N. sp. C*). A total of 12 or 85.7 percent of these parasites was obtained from 3 specimens of *Gerbillus gerbillus;* 2 of them, or 14.2 percent, were found on 1 specimen of *G. pyramidum.* One female specimen, *Ng. A, N. sp. B,* was found on host No. 47, *G. pyramidum,* in a barren desert area. Another new genus and species, *Ng. A, N. sp. E,* found on 2 rodents in the same area, consisted of a nymph recovered from host No. 86, *Meriones crassus,* and 1 female and 3 nymphs removed from host No. 166, *Jaculus jaculus.* A total of 17 specimens of *Androlaelaps marshalli* Berlese (4♂♂; 11♀♀; 2 nymphs) was recovered from 4 gerbils, *Gerbillus gerbillus,* in barren regions of the deserts. There were 38 specimens of *Hirstionyssus* n. sp. (9♂♂ and 29♀♀) which were also removed from 4 of these gerbils in similar barren areas. Host No. 20 harbored 12 or 31.5 percent of these mites; Host No. 21 had 16 or 42.1 percent; host No. 28 had 9 or 23.6 percent; and host No. 39 had 1 or 2.6 percent. A single female specimen of *Haemolaelaps murinus* Berlese was found on *Arvicanthis niloticus,* host No. 73, in the cultivated Nile Valley.

LICE

There was a total of 386 lice collected from 4 species of rodents (table 2). Of this number 379 (53♂♂; 47♀♀; 279 nymphs) were *Polyplax abyssinica* Ferris and 7 (3♂♂ and 4 nymphs) were *P. gerbilli* Ferris. In the cultivated Nile Valley 12 kusu rats, *Arvicanthis niloticus,* harbored 356 specimens (93.9 percent) of *Polyplax abyssinica* (50♂♂; 42♀♀; 264 nymphs). This was an average of 29.7 lice per rat. In the barren regions of the deserts 8 or 2.1 percent of these lice were found on *Gerbillus gerbillus;* 2 or 0.5 percent on *G. pyramidum;* and 13 or 3.4 percent on *Jaculus jaculus.* In the same regions a total of 3 specimens of *Polyplax gerbilli* (1♂ and 2 nymphs) was found on a gerbil, *Gerbillus pyramidum* and 4 (2♂♂ and 2 nymphs) were found on another specimen of *G. pyramidum.*

NESTS

A total of 87 rodent nests was examined for ectoparasites. There were 7 with 120 ticks (5 larvae; 90 nymphs; 15♂♂; 10♀♀). This number included

TABLE 2.—Kinds and number of mites and lice collected on 9 species of rodents.

Hosts	No. of Mites collected	Androlaelaps marshalli	Bdellonyssus bacoti	Haemolaelaps murinus	Hirstionyssus n. sp.	New genera and species	No. of Lice collected	Polyplax abyssinica	Polyplax gerbilli
Arvicanthis niloticus	51	0	50	1	0	0	356	356	0
Gerbillus gerbillus	103	17	17	0	38	31	8	8	0
G. pyramidum	10	0	4	0	0	6	9	2	7
Jaculus jaculus	10	0	5	0	0	5	13	13	0
Meriones crassus	60	0	0	0	0	60	0	0	0
Jaculus orientalis	12	0	12	0	0	0	0	0	0
Meriones shawi	6	0	6	0	0	0	0	0	0
Psammomys obesus	0	0	0	0	0	0	0	0	0
Nesokia indica	0	0	0	0	0	0	0	0	0
Total	252	17	94	1	38	102	386	379	7

95 specimens of the argasid tick, *Ornithodorus erraticus,* (5 larvae; 65 nymphs; 15♂♂; 10♀♀) which were collected from 4 nests in empty burrows in the cultivated Nile Valley. The same area yielded 25 nymphs of the ixodid tick, *Haemaphysalis leachii;* these were found in a single nest also removed from an empty burrow.

A total of 40 fleas, *Xenopsylla cheopis,* (Roths.) was found in 7 nests (19♂♂ and 21♀♀). Of this number 38 (18♂♂ and 20♀♀) were collected from 6 nests of the kusu rat, *Arvicanthis niloticus,* in the cultivated Nile Valley; 2 were found in a nest in an empty burrow in a barren area of the desert. (There were 163 undetermined flea larvae recovered from 5 nests of the kusu rat and 33 from 2 nests in empty burrows).

A total of 284 parasitic mites (11♂♂; 100♀♀; 173 nymphs) was collected from 22 nests. One male specimen, *Androlaelaps marshalli,* was found in an unoccupied nest in a barren portion of the desert. Of the 169 specimens of *Bdellonyssus bacoti* recovered from 12 nests (23♂♂ and 146 nymphs), 14 (7♂♂ and 7 nymphs) were found in 4 nests occupied by *Arvicanthis niloticus* in the cultivated Nile Valley. The remainder, 155, consisting of 16♀♀ and 179 nymphs were found in 8 nests. A total of 11♀♀ and 93 nymphs of *B. bacoti* was found in 5 nests in empty burrows in the cultivated Nile Valley; 5♀♀ and 46 nymphs were found in 3 nests in empty burrows in barren regions of the deserts. One female specimen of *Haemolaelaps* n. sp. was found in a nest of *Arvicanthis niloticus* while 8 of them (2♂♂ and 6 nymphs) were taken from empty burrows. A total of 25 specimens of *Haemolaelaps inops* var. *zulu* Berlese (2♂♂; 18♀♀; 5 nymphs) was collected from 3 nests of *Arvicanthis niloticus* in the cultivated Nile Valley; the remaining 50 (3♂♂; 32♀♀; 15 nymphs) were found in 2 nests in empty burrows. Of the 13 new genera and species (1♂; 11♀♀; 1 nymph), 3 specimens were found in a single nest of *Arvicanthis niloticus* in the cultivated Nile Valley; 9 were in a single nest of *Gerbillus gerbillus* in a barren area of the desert; and 1 specimen was recovered from a single nest in an empty

burrow in a similar region. The 17 specimens of *Steatonyssus viator* (Hirst) (2♂♂ and 15♀♀) were also found in a single nest in an unoccupied burrow in a barren portion of the desert. Free-living oribatid and phytoseid mites (559 specimens) were predominant in nests found in empty burrows.

A total of 12 lice (4♂♂; 1♀; 7 nymphs) was also recovered from 3 nests in barren areas of the deserts. One nest of *Gerbillus gerbillus* had 3 specimens of *Polyplax abyssinica* (1♂ and 2 nymphs); another nest of the same species of rodent had 5 specimens of *P. abyssinica* (2♂♂; 1♀; 2 nymphs). A single nest of *Gerbillus pyramidum* had 4 specimens of *Polyplax gerbilli* (2♂♂ and 2 nymphs).

Of the 87 nests examined for ticks, fleas, lice, and mites, 40 or 46.4 percent (exclusive of the undetermined flea larvae) yielded 1015 specimens (456 ectoparasites and 559 free-living mites).

Specimens of the following arthropods were also found in nests removed from occupied and unoccupied rodent burrows. Their occurrence was probably incidental.

COLEOPTERA. Dermestidae: *Attagenus* sp. Ptinidae: *Gibbium psylloides* (Czemp.) in nest of *Arvicanthis niloticus*. Cucujidae: *Laemophloeus* sp. Staphylinidae: *Tachyporus* sp. in nest of *Arvicanthis niloticus; Trogophlaeus* sp. in nest of *Arvicanthis niloticus*. Coccinellidae: *Rhizobius chrysomeloides* (Hbst.) in nest of *Arvicanthis niloticus*. Curculionidae: *Sitona* sp. nr. *crinitus* Hbst. in nest of *Meriones crassus*. Tenebrionidae: *Blaps* sp.; *Eurycaulus hirsutus* Mill.; *Platynosum paulinae* Muls. Histeridae: *Saprinus* sp. Nitidulidae: *Carpophilus* sp. Lathridiidae: *Holoparamecus kunzei* Aube; *Migneauxia crassiuscula* (Aube).

HYMENOPTERA. Formicidae in nest of *Arvicanthis niloticus*: *Tetramorium simillium* (F. Sm.); *Pheidole* sp.; *Cardicondyla* sp.; *Solenopsis* sp.; *Monomorium* sp.

CORRODENTIA. Atropidae: *Lepinotus* n. sp.

DIPTERA. Muscidae: *Fannia* sp. (Larvae) in nest of *Psammomys obesus*. Drosophilidae: *Drosophila melanogaster* Mg. Sphaeroceridae: *Leptocerca* sp. in nest of *Meriones shawi*.

LEPIDOPTERA. Pyralididae: *Aglossa* sp. in nest of *Psammomys obesus*. Cosmopterygidae: *Pyroderces* sp. Tineidae: *Tinea* sp.

EMBIOPTERA. In nest of *Arvicanthis niloticus*. *Oligtoma nigra* Hag.; *Embyia savigny* Westwood; *Haploembyia solieri* Westwood.

THYSANURA. In nest of *Meriones crassus*. *Ctenolepisma targionii* Grassi & Rovelli; *C. michaelseni* Escherich.

DISCUSSION

Climatic factors that exist within a burrow are much different from those that prevail outside. Burrow humidity was always higher than that of the atmosphere outside while atmospheric temperature was always higher outside than that within the burrow.

The species composition of ticks on the several rodents did not vary greatly. In the barren and coastal regions of the deserts *Hyalomma* sp. was predominant on rodent hosts; in the Wadi Natroun, *Hyalomma dromedarii;* and in the cultivated Nile Valley, *Ornithodorus erraticus* and *Haemaphysalis leachii.* These ticks did not exhibit host-specificity, *Hyalomma* sp. having been obtained from 6 species of rodents, and, a total of 18 *H. dromedarii* from 2 species of rodents. The remainder were too few in number to be considered from the point of view of host-specificity. Of the 146 ticks recovered from their hosts,

larvae and nymphs (65 and 56 respectively) were taken more frequently than mature specimens (11 ♂♂ and 14♀♀).

Ioff (1941) states that the number of female fleas is almost always higher than males in collections recovered from animals. Of the 365 fleas collected during this study, however, the sex ratios were approximately equal, 174♂♂ and 191 ♀♀. With the exception of 10 specimens these fleas were restricted to the cultivated Nile Valley and barren desert areas, thereby occupying comparatively large areas of territory populated by their hosts. The cosmopolitan rat flea, *Xenopsylla cheopis,* was predominant but not highly host-specific. It was found on 4 species of rodents in the cultivated Nile Valley and barren desert regions. Most of them (93) were recovered from 9 specimens of *Arvicanthis niloticus* and had a *cheopis* index of 10.3 per rat. *Xenopsylla conformis mycerini* was the only flea found in large numbers (125) that showed specificity of host selection. It was found only on Sundevall's jird, *Meriones crassus,* and had a parasite index of 13.8 per rat. Opportunity for its transfer to other species of rodents, on the other hand, may have been lacking or there may have been physiological restrictions. The third largest group of fleas collected, *Synosternus cleopatrae,* did not exhibit any evidence of host specificity having been recovered from 5 host species. The flea fauna did not show a considerable range in specificity of host selection. Multiple infestations, however, were observed on 10 hosts. A total of 9 of these hosts were infested by 2 species of fleas; host No. 189, *Meriones crassus,* was infested by 3 species. The microclimate of the habitats had temperatures that ranged from 77° to 108° F and relatively high humidities, factors more or less favorable for the multiplication of fleas. Ioff (*loc. cit.*) has indicated that for adult fleas 70 to 100 percent humidity may be considered favorable.

Of the 252 mites found *Bdellonyssus bacoti* was the most abundant and also the most widely distributed having been found in the cultivated Nile Valley, the barren areas of the deserts, and the Mediterranean coast. It occurred on 6 different species of rodents and had a *bacoti* index of 6.6 per rat. Although in most parasitic mites the form most abundantly found on the host is the female, we found more nymphal forms than females of *B. bacoti* on the rodents. There were no males. The apparently rare species was *Haemolaelaps murinus,* only a single specimen having been found. Of the 4 new genera and species of mites, the most abundant was *Ng A, n. sp. D* which occurred on 4 species of rodents in barren desert regions and which had a parasite index of 5.5 per rat. *Hirstionyssus* sp. was found in similar areas on 4 gerbils and had a parasite index of 9.5 mites per rat. There was no marked host-specificity in the mite fauna. As a group the gerbils were more heavily infested with them than were the other groups of rodents.

The lice exhibited a rather high degree of host-specificity as compared with the other ectoparasites. Of the 386 lice collected, 356 were found on *Arvicanthis niloticus* in the cultivated Nile Valley. Only 30 lice were found on 3 species of rodents in barren desert regions. Hopkins (1949) considers the appearance of *Polyplax* on rodents, and also on shrews, well authenticated instances of a definite and permanent establishment of a parasite genus on two widely separated groups of hosts. Since *Polyplax abyssinica* was obtained with

much frequency from a given rodent species (*Arvicanthis niloticus*) the probability that it was a normal parasite of this host became more obvious, especially since it occurred in such large numbers. Too few *Polyplax gerbilli* were found (7) to arrive at any conclusions concerning host-specificity.

The heaviest infestations of ectoparasites were found on the following rodents: *Gerbillus gerbillus* and *G. pyramidum*, ticks; *Meriones crassus* and *Arvicanthis niloticus*, fleas; *Gerbillus gerbillus*, *Meriones crassus*, and *Arvicanthis niloticus*, mites; *A. niloticus*, lice.

Since each collection may be considered to represent the parasite index of the burrows, it may be assumed that the collections obtained from the rodents and nests portray the population density and species composition in given areas. The figures, however, do not necessarily indicate population trends, as the number of host records differ for each month, but they do suggest that there may be certain seasonal differences in the relationships of the various ectoparasites to their hosts. These differences may be attributed to several factors. The parasites vary in the length of time spent on the host; some spend all or most of their adult life there, while others may be primarily inhabitants of the burrow or the nest. Since different species of rodents were not found using the same system of burrows we have no specific data to show what opportunity there may be providing for the exchange of ectoparasites to other species. On the other hand, parasite transfer could be effected directly from host to host of the same species utilizing the same burrows or indirectly from nest material and burrow surfaces. The rodents, judging from the evidence ascertained from nests, seemed to be particularly effective in seeding their habitats with parasites, especially mites, with which other rodents might come in contact.

Usually each kind of rodent was restricted to a narrow range of habitat conditions. The kusu rat, *Arvicanthis niloticus*, occurred in proximity to cultivated fields in the Nile Valley. One reason for this appeared to be the availability of seeds of crop plants and weedy grasses as food. The gerbils, Sundevall's jirds, and the lesser Egyptian jerboas were restricted to barren areas in the deserts. *Gerbillus gerbillus* and *G. pyramidum* were usually found at the base of hillocks of wind-blown sand where the burrows could be easily dug. *Jaculus jaculus* occurred in hard clayey-sand slopes devoid of vegetation and *Meriones crassus* was most abundant on the sides of shallow-filled wadis and roadside banks on which various shrubs were growing. In the coastal region of the Western Desert *Jaculus orientalis* and *Meriones shawi* occupied barren isolated sand slopes while the fat sand rat, *Psammomys obesus*, occurred in a semi-desert densely populated with perennial shrubs and dotted with hillocks. The bandicoot rat, *Nesokia indica*, was restricted to the low-lying saline regions of the Western Desert. In the Faiyum the high water table kept the burrows of this rodent damp and the humidity high (maximum humidity 75 percent). Ectoparasites were not found on bandicoots removed from these damp burrows. In the Wadi Natroun, however, where the water table was low, burrows of these rodents were dry and the humidity relatively low (maximum humidity 50 percent). Bandicoot rats removed from these dry burrows were parasitized with ticks.

The rodent populations appeared to be distributed chiefly in relation to type of soil, micro-topographic features, availability of suitable food plants, and micro-climatic conditions, especially humidity within the burrows.

SUMMARY

A survey was made to determine the kinds and distribution of wild rodents and their ectoparasites and to provide preliminary data on relationship to temperature, humidity, soil and vegetation conditions in Egypt.

The areas investigated were the cultivated Nile Valley, and the Eastern and Western Deserts.

The kusu rat, *Arvicanthis niloticus,* was found chiefly in proximity to cultivated fields in the Nile Valley. *Gerbillus gerbillus, G. pyramidum, Jaculus jaculus,* and *Meriones crassus* were restricted to barren desert regions. *Jaculus orientalis, Meriones shawi,* and *Psammomys obesus* were located in the coastal area of the Western Desert. The bandicoot rat, *Nesokia indica,* was restricted to the low-lying saline areas in the Western Desert.

A total of 178 rodents, including 9 species, was collected.

The chief factors governing the distribution of these rodents were the type of soil, micro-topographic features, availability of suitable food plants, and micro-climatic conditions, especially humidity within the burrows.

Humidity was always lower and temperature always higher outside of the burrows than those within the burrows.

A total of 1149 ectoparasites representing 23 species was collected during July, August, September, and part of October, 1953. Of this number 365 fleas were recovered from 56 rodents; 146 ricks from 30 rodents; 252 mites from 7 rodents; and 386 lice from 4 rodents.

Nests examined for ectoparasites yielded 120 ticks; 40 fleas; 284 mites; and 12 lice. The nest afuna also included 559 free-living mites (oribatids and phytoseids) and miscellaneous arthropods representing 7 orders.

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A Clarification of the Species of the Genus Typhloplana

John G. Mahan
Lynchburg College, Lynchburg, Virginia

The first *Typhloplana* was described by P. C. Abildgaard in the year 1789, although the genus name originated with Ehrenberg in 1831. The former date was only forty-five years after the first turbellarian, a freshwater planarian, had been described by Trembley. Due to the crudeness of technique at that time many genera which were named during that period have since been combined as one genus or lost as species of other genera. Such for some time seemed the fate for which the genus *Typhloplana* was destined since it first became a repository for any turbellarian which lacked eyes or appeared to lack them, then a similar catch-all for those species having zoochlorellae in their mesenchyme, and finally was considered to be a genus of the Order Tricladida, Family Planariidae. Schultze in 1851 placed it in the superfamily Eumesostominae recognizing its true rhabdocoele position, and Luther in 1904 in the creation of the two families of the Eumesostominae, the Mesostomidae and the Typhloplanidae, gave it its final rightful position. Luther (1904, Part II, p. 172) likewise clearly fixes the generic characteristics with the following description:

> Typhloplanidae without eyes, with an excretory cup, two (or one) uteri, without an atrium copulatorium and bursa copulatrix, receptaculum seminis inserted in the oviduct, without dermal rhabdites.
>
> Both species of this genus are very similar so that in most cases they resemble one another closely. The genus shows a great resemblance also to the genus *Castrada* in the possession of erythrophil cephalic glands found only in these two genera. The single essential difference appears in the lack of an atrium copulatorium and the bursa. I am forced to assume that the loss of this organ has been brought about through degeneration and that the *Typhloplana* species have descended from *Castrada*-like ancestors.

Such have remained the distinguishing characteristics of the genus since 1904, later writers accepting Luther's delineation of the genus as the basis for their creation of species. There seems to be no reason for questioning the validity of the genus as it now stands, though it may be that, at the present time, transition forms between *Castrada* and *Typhloplana* still exist which, though definitely belonging to the latter genus, yet retain some characteristics of the former.

Even more numerous than the genera have been the species to which typhloplanae have been assigned. Abildgaard recognized only one species, *Typhloplana* (or *Planaria*) *viridata,* but since 1831 nineteen new species of *Typhloplana* have been named, of which at least eighteen have turned out to be, on later examination, representatives of other genera if not of other families or orders. The only valid species created was *Mesostoma minima* which was so named by Fuhrmann in 1894 and renamed *Typhloplana minima* by Luther in 1904.

As of 1945 then, two species remain, *Typhloplana viridata* and *Typhloplana minima.* It would be supposed that these two species would be clearly delineated, but since 1904 there has been no certain method of distinguishing between

the two. In way of illustration I shall present here in their chronological order the specific differences as given by various authors from which the dubiety of the classification may be gathered.

In the original paper by Luther (in 1904, p. 174), in which the two species are mentioned separately for the first time he was able to describe specimens of *T. viridata* only with winter eggs and specimens of *T. minima* only with summer eggs and concludes his summary with this remark: "It seems to me not wholly out of the question that both of these existing forms might be included in a single species, but I must leave the decision on this to the future."

Hofsten (1907) would distinguish between *T. viridata* and *T. minima* on the basis that in the former the penis opens into a dorsal part of the genital atrium which is bounded ventrally by a strong sphincter and which he considers to be a vestige of the atrium copulatorium found in the *Castrada* species, while in the latter the penis opens directly into the genital atrium without the mediation of a separate atrium copulatorium. However, in another paper Hofsten (1911), in giving a description of some specimens which he had classified as *T. viridata,* states: "My specimens which were all filled with summer eggs corresponded closely with the description by Luther (1904) of *Typhloplana minima;* nevertheless I placed it as *T. viridata* since according to the foregoing description the two species may not be distinguished from one another. Brinkmann (1905) is, therefore, at least for the present in the right when he regards the two forms as identical."

Von Graff (1913) gives the following specific differences in his Key to the Species (p. 225):

"Vitellaria very large, testes lateral to pharynx, the large rhabdites blunt on their ends, dorsal atrium usually beset with spines ....*T. viridata*

"Vitellaria small, testes posterior to pharynx, the large rhabdites pointed on their ends, atrium shows no spines ....*T. minima.*"

He then proceeds to add in a footnote: "According to Volz (1901), Sekera (1904), and Brinkmann (1906), the two species may be considered to be identical. The last-named (Brinkmann) considers *T. minima* to be the spring form arising from winter eggs, *T. viridata* to be the summer generation arising from summer eggs of a single species."

Other authors have followed the suggestion made by von Graff that the distinguishing character be the presence of two uteri in *T. viridata,* one in *T. minima,* and on this fallacious basis of distinction the question has rested until the present time, each investigator using whatever particular distinctive character he saw fit and accepting the opinion of one of the men mentioned without investigating the matter for himself.

As an example of the confusion existing, Higley (1918) describes *Typhloplana "viridata"* collected in the Mississippi basin but describes for it vitellaria corresponding in size to those which von Graff has assigned to *T. minima.* She closes her brief consideration of her specimens with the statement that "from the several descriptions given by different authors and in the above details, it would appear that this species undergoes a greater amount of variation than is possible in many forms."

It will be clearly apparent from the various accounts given above that though the genus has been firmly fixed for over forty years there is need for

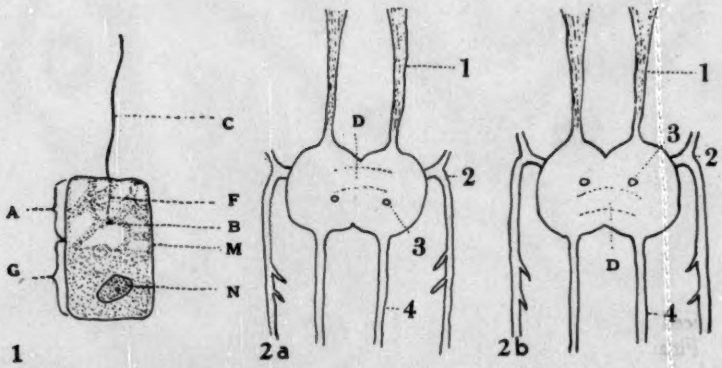
some definite and final criterion for distinguishing between the two species, if two there be. Pratt (1935) recognizes only *T. viridata* and practically all recent works have done the same. However, if two species exist they should both be given recognition, the morphological similarities and differences between them should be given, and any physiological points of comparison should be taken into consideration.

My interest in the problem stemmed from the finding of specimens in Mountain Lake, Giles County, Virginia, whose reproductive methods appeared divergent from those of lowland specimens collected from Plum Run in Gettysburg, Pennsylvania. This discovery led to a physiological examination of them in the living condition and to a later fixing, staining and examination of each group from a morphological standpoint. The latter aspect of the comparison will be considered first and is represented by the accompanying chart in which the two are represented in parallel columns and by figures 1-9.

	GETTYSBURG SPECIMENS	MOUNTAIN LAKE SPECIMENS
Epidermis	Continuous over whole exterior of body, invaginated for short distance into mouth opening and genital pore. Uniform coat of cilia. Cells consist of outer alveolar layer and inner granular layer containing the nuclei. Granular portion destroyed and syncytium appears in pregnant forms.	General structure same. No destruction of any part of epidermis at any period during life.
Musculature	Thin outer layer of circular muscle and inner layer of longitudinal muscles. Retractor muscles extending from region of pharynx to anterior tip. Retractors relatively poorly developed.	Same as in Gettysburg specimens.
Mesenchyme	Mesenchyme consists of "hyaloplasm" and "spongioplasm," the latter being more abundant in regions of considerable pressure, the former where pressure is less. Average number of mesenchymal cells in cross-sections 7μ thick, 28-32. Zoochlorellae numerous, lying in interstices of mesenchymal net; average size of zoochlorellae 2μ in diameter.	Same as in Gettysburg specimens.
Nervous system	"Brain" composed of two ganglia joined by a commissure in their anterior dorsal portions. Heavy cortex dorsally and laterally, very thin ventrally. Four main nerve tracts, one directed anteriorly, one postero-laterally, one dorsally, one posteriorly. Nerve III located just posterior to commissure.	Commissure located farther posteriorly than in Gettysburg specimens. Nerve III issues from brain anterior to the commissure. Crescent-shaped body dorsal to commissure which is believed to be a vestigial light-sensory structure though bearing none of the elements of a retinula.

	GETTYSBURG SPECIMENS	MOUNTAIN LAKE SPECIMENS
Digestive system	Consists of mouth opening at end of anterior third of body, pharyngeal chamber, pharynx with intrinsic and extrinsic glands, esophagus, and enteron. Pharynx rosulatus, containing circular, longitudinal, and radial muscles. Enteron composed of non-ciliated columnar endodermal cells, with no specialized gland cells.	Same as in Gettysburg specimens.
Excretory system	Excretory cup set in mouth, receiving openings of protonephridial stems laterally. Protonephridial stems divide on either side into an anterior and a posterior branch which is lost in the tissues of the mesenchyme. No evidence of secondary branches or of flame cells. Position of excretory cup relative to mouth opening variable.	Same as in Gettysburg specimens.
Reproductive systems	Common genital pore just posterior to mouth opening; common genital atrium. Male system composed of paired testes and vasa deferentia, single vesicula seminalis and penis. Female system composed of a single ovary, oviduct, receptaculum seminis, ductus communis, and shell glands; paired vitellaria and uteri, both opisthodelphous. No evidence of a separate dorsal portion to the genital atrium.	Common genital port just posterior to mouth opening. Genital atrium has a ventral portion receiving openings of genital pore, two uteri, dorsal atrium, and ductus communis. Dorsal portion of atrium closed off by a weak sphincter; receives penis. Other structures, male and female, same, except that shell glands are better developed than in Gettysburg specimens.
Reproduction	Only observed method by growth of embryo within body of mother, embryo feeding on organs and tissues of mother until she is only a ciliated sac. Mother destroyed in birth of young. Embryos may number 2-7. Young born with zoochlorellae acquired from mesenchyme of mother.	Reproduction only by laying of hard-shelled eggs which are deposited through the genital pore after a period of intrauterine development. Mother not destroyed by laying of eggs. Three to five eggs in uterus at a time. Young do not have zoochlorellae at hatching but acquire them by feeding on disintegrating *Typhloplanae* in the water after hatching.

The chief morphological difference to be noted here is the presence in the Gettysburg specimens of a *common* genital atrium which receives both the penis and the oviduct, while in the Mountain Lake specimens the penis opens into a dorsal part of the genital atrium which is closed off from the ventral portion which receives the ductus communis by means of a weak muscular sphincter.



Figs. 1, 2.—1. Drawing of epidermal cell. C, cilium; F, fibril; B, blepharoplast; M, cell membrane; N, nucleus showing nucleolus; A, alveolar portion of cell; G, granular portion of cell. 2. (a) Diagram of dorsal aspect of "brain" and four main nerve stems of *Typhloplana minima.* (b) Diagram of dorsal aspect of "brain" and four main nerve stems of *Typhloplana viridata,* s.sp. *ovipara.* I, II, III, and IV are nerves; D, dorsal commissure.

Also interesting and productive of speculation are the changes undergone by the pregnant forms during the development of the embryos in the case of the Gettysburg specimens. In the first place, the embryos remain in the uterus for only a short period. Thereafter, their growth reaches a point where they burst through the wall of the uterus and are released into the mesenchyme. There they feed on the mesenchyme and the internal organs indiscriminately, eventually eating out all of the inside of the mother animal. However, the mother herself contributes to their growth to a slight extent by the dissolution of the inner granular, nucleated portion of the epidermis, so that by the time

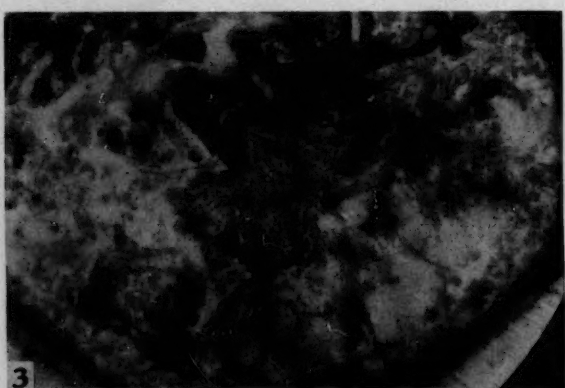


Fig. 3.—Photomicrograph of cross-section of "brain" of *Typhloplana viridata,* s.sp. *ovipara,* showing cortical and medullary portions and crescent-shaped body dorsal to commissure. Note long cilia and two portions of epidermal cells. ×680.

the embryos break through the thin epidermal wall the mother has been reduced to a ciliated sac (fig. 9).

Finally, the crescent-shaped body dorsal to the dorsal commissure of the brain in the Mountain Lake specimens and which is believed to be a vestigial light-sensory structure may have importance as an indication that the typhloplanae are degenerate forms of a group which at one time possessed functional eyes (fig. 3).

PHYSIOLOGY

As mentioned above, my interest in the problem stemmed from a difference in reproductive methods which had been noted between specimens of *Typhloplana* collected at Mountain Lake, Virginia, and those collected at Gettysburg, Pennsylvania. The former, collected and studied at different periods between June and August inclusive in shallow water, always contain only hard-shelled eggs; the latter, collected between June and August likewise, in Plum Run, a small stream on the Gettysburg battlefield, contain only embryos and show no development of winter eggs.

The problem presented then was as to whether the two forms distinct in their reproductive methods, were one and the same species, the difference being due to environmental factors, or whether they were entirely different species. It was first assumed that the difference might be one of water temperature, since Gettysburg is in a lowland area while Mountain Lake is at an altitude of four thousand feet. With this in mind it was proposed to subject specimens from each environment to the water temperature of the other with the idea

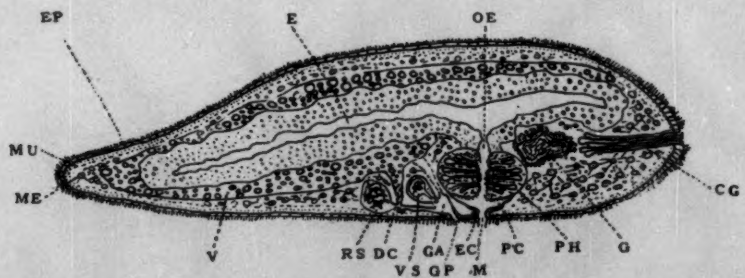
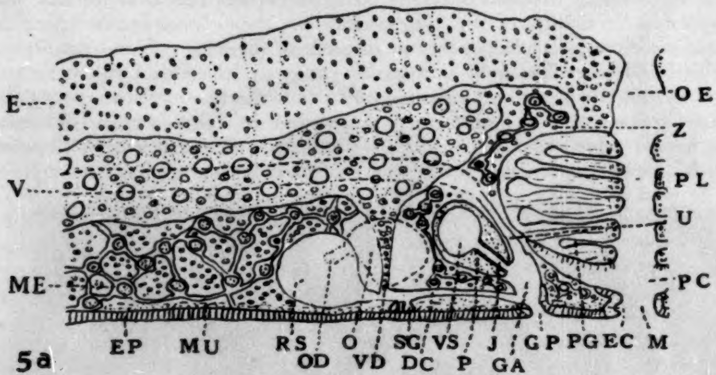


Fig. 4.—Drawing of sagittal section of *Typhloplana minima* from right side. CG, cephalic glands; DC, ductus communis; E, enteron; EC, excretory cup; EP, epidermis; G, ganglia; GA, common genital atrium; GP, common genital pore; M, mouth opening; ME, mesenchyme; MU, muscle layers; OE, esophagus; PC, pharyngeal chamber; PH, pharynx; RS, receptaculum seminis; V, vitellarium; VS, vesicula seminalis.

that the method of reproduction might be changed in this fashion. Water temperature at Gettysburg in the area in which specimens were collected was found to be 21°C. Animals collected at Mountain Lake were raised to that temperature with the hope that their reproductive methods would be changed. The water temperature of the portion of the lake in which they live is 18°C during the months of their collection.

A rise of three degrees (from 18-21°C) produced no change in their

methods of reproduction. The temperature of 21°C was maintained for two to three weeks and no apparent inconvenience was noted in the specimens as a result. With the thought that possibly a higher temperature would produce better results, it was raised to 24° and then to 26°C and kept at each of these temperatures for a three-week period. The specimens throve at both these temperatures but showed no modification in their method of reproduction. The higher temperature is greater than any encountered even in sunny water at



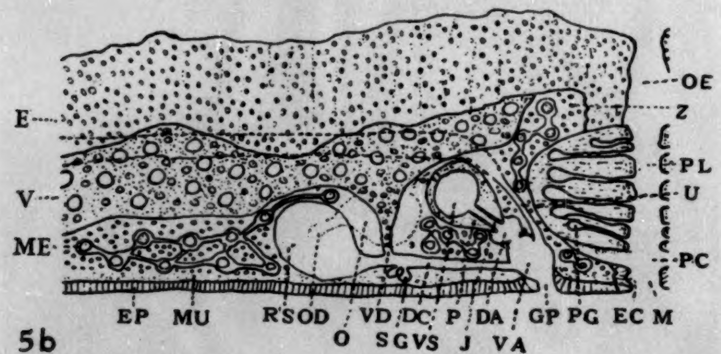
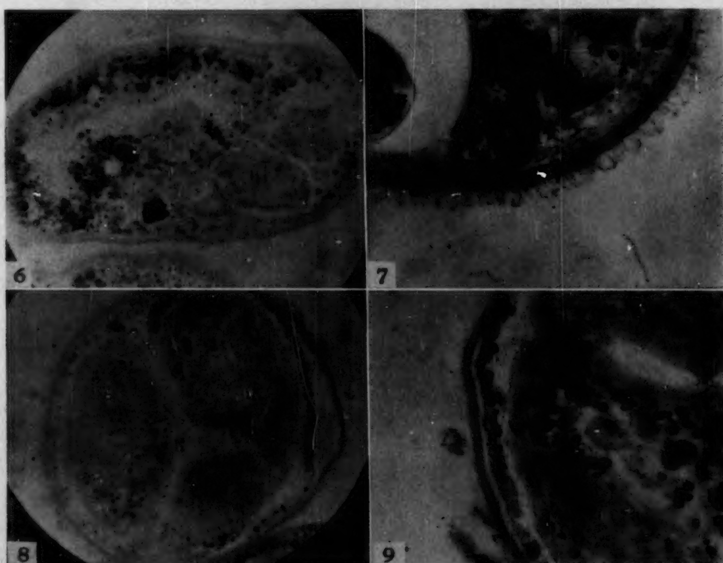


Fig. 5.—(a) Drawing of sex organs of *Typhloplana minima*, showing an enlarged section of figure 4. (b) Drawing of sex organs of *Typhloplana viridata*, s.sp. *ovipara*, showing the dorsal and ventral portions of the genital atrium. DA, dorsal atrium; J, ductus ejaculatorius; O, ovary; OD, oviduct; P, penis; PG, pharyngeal glands; PL, lumen of pharynx; SG, shell glands; U, uterus; VA, ventral atrium; VD, vitelloduct; Z, zoochlorellae. Others as in legend for fig. 4.

Gettysburg and the period longer than is required to convert animals of closely related genera from viviparity to oviparity, so that it is obvious that temperature does not serve to produce the result.

Hallez (1890), working with two *Mesostoma* and one *Bothromesostoma* species, claimed that in these two genera the production of summer eggs took place while the animals were in abundant water, while as soon as the water

began to evaporate a change to the laying of winter eggs occurred. I attempted to reverse this experiment, working from the winter to the summer condition, as he had successfully done with the two genera mentioned above; that is, I added fresh water to the animals, removing the old and constantly increasing the amount of water. I met with no success and was not able to duplicate his experiments. My belief on the explanation of Hallez's results is that as evaporation of water occurs the concentration of waste matter and debris in the water remaining increases, with the consequence that conditions become less favorable for the life of the Mesostomida and they change to the laying of hard-shelled eggs which are better adapted to surviving adverse conditions. This could be verified only by a test of changes in the pH of the water and an analysis of organic and inorganic contents at the time. My equipment for carrying out such tests was scanty and I noticed little change in the pH from its normal value of 7.3 for the water in which the specimens occur. Likewise, no Mountain Lake animals for the whole of their "spring" and summer periods



Figs. 6-9.—6. Photomicrograph of sagittal section of *Typhloplana minima,* taken through mouth and genital pore. ×250. 7. Photomicrograph of portion of cross-section of *Typhloplana viridata,* s.sp. *ovipara,* showing shelled egg in uterus on left, opening of uterus, ventral atrium to right of uterus, portion of dorsal atrium dorsal to the ventral atrium, and ovary to right of uteri. Note two portions of epidermal cells and long cilia covering epidermis. ×475. 8. Photomicrograph of cross-section of pregnant specimen of *Typhloplana minima.* Two embryos with pharynx showing in each toward top and left. Vitellarial material in mesenchyme of embryos and surrounding them. Mesenchyme of mother ventral and median to embryos. Note that only alveolar layer of epidermis is present in the parent. ×250. 9. Photomicrograph of same section as above to show epidermis. ×475. Note that only alveolar layer of epidermis with blepharoplasts and cilia remains. Compare with figs. 3 and 7.

produce their young alive, the hard-shelled eggs being the only method of reproduction found.

An interesting experiment was conducted on the young which hatched from the hard-shelled eggs. Two of these eggs were isolated in a small dish which contained fresh water but in which no adults had been. Upon hatching the young were colorless, and reared through a period of two weeks remained colorless. During this time they were fed on diatoms and segments of annelids but had no contact with anything green. The specimens died before reaching full size but had never shown any trace of greenness.

Two other eggs were left in the dish with the adult animals. These upon hatching were likewise colorless but within a few hours were observed feeding upon the remains of disintegrating specimens which were in the water. Within twenty-four hours they appeared a pale green, and in seventy-two hours they were the same color as the adults though still small.

From this it seem obvious that no zoochlorellae are contained within the hard-shelled eggs and that in a normal existence the young obtained from these eggs get their zoochlorellae from the process of feeding on the disintegrating animals in the water in which they live, or from the surrounding pond water.

Any attempt to reverse either of the experiments mentioned above, namely, the lowering of the temperature for the Gettysburg animals, or the subjection of them to evaporation of water, was impossible, since during the summers of 1944 and 1945 searches in the Gettysburg area and likewise in the Charlottesville, Virginia, area produced no specimens for study in the living condition. This fact is to be regretted but does not carry too much weight in the light of morphological study which indicates the two forms to be different species.

CONCLUSIONS

From the above it will be obvious that at least two species of the genus *Typhloplana* exist, and that the more recent publications which recognize only *T. viridata* as a species are incorrect. It might be considered by some that the Mountain Lake specimens which produce only hard-shelled eggs represent only a later-seasonal form of the Gettysburg specimens, or, in other words, that there is an earlier period during which the Mountain Lake animals produce their young alive. However, it should be noted that June represents middle spring at the altitude of four thousand feet, while July is the only month without freezing temperatures. Hence, if there were any two months in which one would expect to find animals in their summer condition those months would be June and July. Yet in both these months only hard-shelled eggs are found in these animals.

No Gettysburg specimens have been collected during September or October and hence none has been found which contained winter eggs. I have no doubt that such forms do exist during these months, the eggs remaining dormant throughout the winter period and hatching in the spring to produce that year's generation. It would be extremely difficult for the animals to survive the adverse conditions of temperature found in Gettysburg in the fall and winter months, and this would be even truer in the case of the young, recently born animals. Hence, a resting winter stage represented by hard-shelled eggs formed in the late months of Summer and the early months of Fall seems the best explanation of the survival of the species over the winter period.

With regard to the Mountain Lake form the cause of the lack of a viviparous stage must be conjectural. The extreme brevity of the warm period there would seem to be a possible explanation. However, during that period when the water is warm it is equally as warm as that in which lowland specimens are found. It is true that the diurnal variations in temperature are greater at Mountain Lake than in any lowland locality, but since water responds rather slowly to changes in air temperature it would seem hardly likely that there would be more than ten degrees difference in the water temperature at any time during the months of June and July. I have taken the water temperature in bright sunlight, on cloudy days, in fog, and at night, and have never found more than five degrees difference between the maximum and the minimum. The lowest (16°C) was found during a fog, and the highest (21°C) in the afternoon on a bright day.

Although Mountain Lake is subject to slight variations in depth, these variations ordinarily amount to no more than an inch or two, so that lack or abundance of water could not account for the change.

Von Graff (1913) states that both *Typhloplana viridata* and *Typhloplana minima* reproduce viviparously during a phase of their lives. On this basis the Mountain Lake form would belong to neither of these two species. However, Hofsten (1907) distinguishes between the two species on the basis that in *T. viridata* the penis opens into a dorsal part of the genital atrium which is bounded ventrally by a sphincter, while in *T. minima* no such sphincter or dorsal portion of the genital atrium is present, the penis opening directly into the common genital atrium.

Combining these two points of view, neither of which has been modified since its statement. I state that the Gettysburg form is *Typhloplana minima*, unmodified and corresponding completely with the description of this species given by all authors. The Mountain Lake specimens represent a physiologically modified form of *Typhloplana viridata* which, though corresponding morphologically with all descriptions of the species previously given, have lost the viviparous stage of their life-cycle. I propose no change in species names. However, I do propose that both *Typhloplana viridata* and *Typhloplana minima* be reinstituted as valid species, and I suggest that the Mountain Lake form be designated a subspecies of the species, *Typhloplana viridata*, and be termed *Typhoplana viridata*, s.sp. *ovipara*.

Acknowledgement.—I wish to express my appreciation to Dr. W. A. Kepner, Professor Emeritus of Zoölogy at the University of Virginia, for the assistance he rendered me in the solution of this problem.

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The Catenula of the Eastern United States

John W. Nuttycombe
University of Georgia, Athens

With the exception of *Stenostomum* and *Dalyellia, Catenula* is probably the most common genus of rhabdocoel encountered in the eastern United States. Collection records indicate the genus *Catenula* to be equally prevalent over the entire eastern part of the country. At present there is no single piece of literature available which would make identification easy or even possible.

The following treatment of the genus *Catenula* is an attempt to evaluate the species known to the United States and to so describe and figure them as to make accurate identification possible. Included are descriptions of two new species and notes on distribution, collection, general biology, culture methods, and a key to the American species so far known.

The genus *Catenula* was established in 1832 by Dugés for a fresh-water worm which he collected in autumn, 1830. He proposed the name *Catenula* because of the resemblance of a specimen of several zooids to a small chain; the specific name *lemnae* was used because he had discovered the animal in a lens of water. Dugés' description is somewhat incoherent and is confused by the fact that throughout the paper he becomes involved in comparisons with tapeworms, other flatworms, and annelids. However, his figures are good and, with the description given, he established beyond doubt the fact that he was dealing with the same species we have cultured for seven years.

Leidy (1851) described *Anortha gracilis* from Philadelphia which so early as 1854 was recognized by Leuckart as a *Catenula* and carried by him as *Catenula gracilis*. *Catenula gracilis* was carried as a species by practically every author who mentioned the genus until Graff (1913) relegated it to synonymy with *Catenula lemnae*. From Leidy's description it is difficult to see how it was specifically identified at all.

Schmarda (1959) added *C. bina* and *C. quarterna* to the genus. *C. bina* lacked a statocyst and *C. quarterna* had a protonephridial tube down each side of the body. However, the description of *C. quarterna* leaves no doubt that Schmarda was dealing with an organism of the same general structure as a *Catenula*. It was suggested by Beauchamp (1919) that such a protonephridial condition would justify removal to another group. Luther (1907) suspected that Schmarda had committed an observational error with reference to the two protonephridial tubes, and Marcus (1945a) considers the inclusion of *C. quarterna* as a valid species open to question but, nevertheless, includes it in his key for the genus. In view of the fact that this species conforms so completely in other respects to the generic criteria, it seems logical that these criteria be revised to allow the inclusion of this species.

Graff (1882) moved *C. lemnae, C. gracilis, C. bina,* and *C. quarterna* into the genus *Stenostomum* in the family Microstomidae, but in 1913 he re-established the genus *Catenula* in the family Catenulidae with two species — *C. lemnae* and *C. quarterna*. Since 1913 six species have been described. From Europe Beauchamp (1919) described *C. sekerai* and Reisinger (1924), *C.*

pygmaea. From Virginia, Kepner and Carter (1930) described *C. virginia*. From Brazil, Marcus (1945a) described *C. alitha*, *C. leuca* and *C. macrura*.

Beauchamp (1919) undertook to separate *C. sekarai* from *C. lemnae* on the basis of anatomical features, but particularly on the difference in the histology of the parenchyma. The species with which he was comparing his new species appears not to have been *C. lemnae* but an undescribed species very widely found in the eastern United States. This species is described in this paper as *C. confusa*.

All the species which have been encountered can be easily identified from study of living specimens. Beauchamp (1919) was justified in questioning size as a major factor in specific identification in *Catenula* but it is entirely unnecessary to resort to fixed material for identification. Marked structural differences in the living animal parallel differences in rate of reproduction, response to culture media, and pattern of regeneration.

Considered in this paper are five species of the genus, four of which we have been able to collect and study in large numbers.

PRESENT TAXONOMIC POSITION OF THE GENUS CATENULA

Graff (1905) established the family Catenulidae and named it for the first genus in the group, *Catenula*. The family also included the genus *Stenostomum*. In 1907 Luther reorganized the family so as to include the following genera: *Catenula*, *Lophorhynchus*, *Stenostomum*, and *Rhynchoscolex*. Reisinger (1924) is responsible for the sharp definition of the sub-order Notandropora and for an adequate discussion of the history and the systematic position of the Catenulidae. Meixner (1938) proposed that the suborder Notandropora be removed from the order Rhabdocoela and be given ordinal rank with the name Catenulida. Marcus (1945a) has followed the taxonomic scheme of Meixner in his work with the group. Although Meixner's arrangement has much to commend it the older system is followed in this paper.

The Catenulidae are Notandropora (Catenulida) in which there are usually four to eight nerve stems running posteriorly from the cephalic ganglion or ganglia. The male gonads are follicular. The female reproductive structures consist only of an ovary; there is neither an oviduct nor a female genital pore. Except in *Rhynchoscolex*, sexual reproduction is periodic, and the usual method of propagation is asexual.

For the genus *Catenula* Graff in 1913 laid down the following criteria: cephalic region delimited posteriorly by ciliated pre-oral groove; anterior region of digestive tract differentiated as a simple pharynx; eye-spots absent; statocyst present in the anterior end of each zooid; protonephridial tube mesio-dorsally placed; paired ciliated pits absent. Figure 1 shows diagrammatically the basic features of the genus.

Ruebush (1941) separates the genus *Catenula* on the basis of being composed of a chain of zooids each of which contains a statocyst in its anterior end. Only one platyhelminth, the larval form of *Rhynchoscolex*, could possibly be confused with a *Catenula*. This larva possesses a statocyst but lacks a preoral groove. With the changes suggested the position of the genus seems sound.

Marcus (1945a), in his reorganization of the genus *Catenula*, considered

the fact that the intestine occupies only the middle of the zooid (not continuous from one zooid to the next) to be critical diagnostic feature for the genus. Because *C. pygmaea* has an intestine continuous between the zooids he removed it to the genus *Dasyhormus*. One of his species, *C. alitha*, lacks a statocyst.

It appears to this author that Graff's criteria, with slight modification, would serve quite as well as those of Marcus for a valid, sharply defined genus. The species described in this paper conform to the criteria of both Graff and Marcus.

Numerous collections for this study were made over a period of several years from Georgia, Virginia, North and South Carolina, Tennessee, Florida, Pennsylvania, New York and New Jersey. *Catenula* inhabit permanent ponds, lakes, and ditches that range from almost crystal clearness to stagnancy. Seasonal variations have no marked effect on the prevalence of species.

Satisfactory collections can be made by removing with a large spoon the upper one-half inch of sediment to a jar filled with water from the site of collection. Sediment washed into a jar from submerged vegetation is also a satisfactory source. After the jars have settled, specimens can be obtained from its sides or from the sediment by means of pipette. In such a jar the population tends to increase until extreme stagnation or other factors interfere.

In nature the food of *Catenula* is composed largely of microorganisms and under ideal conditions reproduction is rapid. *C. lemnae* and *C. leptocephala* are readily cultured in wheat grain infusions prepared according to directions given in Needham's *Culture Methods for Invertebrates*, pp.135-136 (1937). *C. confusa* and *C. sekerae* do not culture satisfactorily.

The morphology of all species except *C. virginia* was studied from living and fixed material. Living specimens can be easily studied in water under a cover glass, even at magnifications of 1500. Satisfactory fixation of *Catenula* was very difficult to obtain. Gilson's, Bouin's (65° C), and Helly's fixing fluids were used. Helly's fluid, 15 to 20 minutes, proved the best fixing agent. Specimens were embedded in tissuemat, sectioned at 7 micra, stained for 20 minutes in Harris' haematoxylin, distained in acid dioxane, and mounted in clarite.

Best fixation was obtained with *C. lemnae*. Attempts to prepare satisfactory whole mounts were not successful.

The general body form is thread-like, roughly cylindrical and somewhat dorso-ventrally flattened. The anterior extremity may be rounded or pointed; the posterior end typically narrows gradually to form a blunt point.

The epidermis is ciliated and differs from that of many rhabdocoels in that its cells carry no visible rhabdites. The ciliary length is usually two to four times the epidermal thickness. In sections the epidermis appears to be composed of squamous or cuboidal cells, whereas in the living animal the epidermal cells appear to be cuboidal. The fact that satisfactory fixation is difficult, probably accounts for the differences in the appearance of the fixed epidermis. The cytoplasm of the epithelial cells stains fairly darkly, and the cells contain large vesicular nuclei.

Immediately beneath the epithelium is the longitudinal musculature. This

tissue is fibroid and the spindle-shaped nuclei resemble those of ordinary visceral muscle. These nuclei show no visible karyosomes.

Separating the cephalic region from the remainder of the zooid is a ciliated, pre-oral groove. The cilia in and about this groove are stouter and longer than those of the general ciliary coat and assist in the feeding process. The lateral aspects of the groove set off the cephalic region sharply.

The V-shaped mouth is located mesio-ventrally just behind the pre-oral groove and is bounded by heavily ciliated lips. It opens directly into a ciliated, muscular, elongate pharynx simplex. In section there may be observed on the antero-ventral walls of the pharynx groups of columnar cells containing small, compact nuclei. These appear to be a part of the pharyngeal musculature. Posteriorly the pharynx opens through a weak sphincter into the sac-like enteron. Gland cells are associated with the pharynx and enteron in various arrangements.

The enteric cells observed were mostly columnar with large, basally placed nuclei containing scattered chromatin granules. Occasional goblet-like cells occur among those of the general enteric epithelium. The cytoplasm of these cells is mottled but without obvious vacuoles or granules.

The enteric epithelium is finely ciliated as indicated by the movement of the food content in the intestinal lumen. No distinct musculature has been observed like that immediately beneath the general epidermis.

The pseudocoel, which varies in width in the different regions of the organism, is filled with cells of various sizes and shapes. Some appear stellate, spindle-like and reticular. Radial muscle tissue may transverse the pseudocoel throughout the entire length of the animal. In the pharyngeal and post-pharyngeal regions of the pseudocoel can be observed unusually large cells containing extremely large nuclei having karyosomes and several groups of chromatin material located just under the nuclear membrane. These cells are unquestionably glandular.

Located in the anterior end of each well-developed zooid is a cephalic ganglion from which arises on each side a pair of posteriorly directed nerves. Marcus (1945b) was able to identify additional nerve tracts to the pharyngeal wall and the lateral, ventral and anterior regions of the epidermis. Sections reveal the interior of the ganglia to be fibrous in appearance and the exterior to be composed of nerve cell bodies.

Associated with each ganglion is a refractive, ovoid statocyst which contains a statolith. The statocyst may or may not be embedded in the ganglionic tissue. Marcus (1945a, 1945b) describes and figures the statocyst in *Catenula* on the posterior face of the cerebral ganglion and states (1945a) that Kepner and Carter (1930) were in error in thinking this feature peculiar to *C. virginia*. Marcus has interpreted the central mass to be the cerebral ganglion proper and the cellular peripheral cells as ganglionic. In living specimens the statocyst appears, in many cases, to be embedded in this ganglionic exterior and consequently does not appear to lie on the posterior face of the "brain mass." Kepner and Carter (1930) described the statolith of *C. virginia* as made up of an almost cytoplasm-free cell with a nucleus and a definite nucleolus. Careful studies of all species, except *C. virginia,* fail to show statoliths conforming to the structure described by Kepner and Carter. These studies show the statocyst to be composed of a vesicle filled with a clear, homogeneous mass contain-

ing a structure of permanent shape. In fixed material the statocyst appears to be surrounded by a flat epithelium.

In a disintegrating worm the vesicular membrane ruptures and the clear semi-fluid content escapes. After the rupture of the vesicle, the statolith remains for hours without change in size or shape. Neither observations on its structure nor behavior suggest that the statolith is a nucleus. In fig. 2 are shown statocysts as seen in fixed material of *C. lemnae,* and in fig. 3 are statocysts from living specimens of *C. leptocephala.*

In living specimens the diameter of the statocysts of any given species is fairly constant for zooids in the same stage of development. Statocysts in different zooids of the same chain differ in size. Measurements of the anterior statocysts in the several species range in diameter from .008 to .02 mm. The statoliths range from .004 to .016 mm in diameter.

The excretory system has been described in detail by Sekara (1924) and by Marcus (1945b). It is similar to that of *Stenostomum* in which there are two mesio-dorsally located tubes.

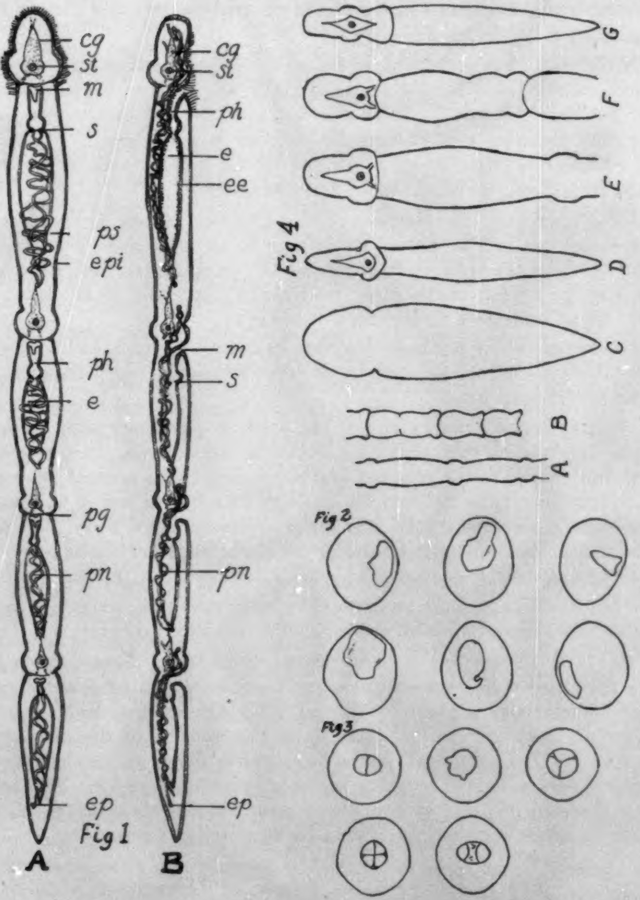
Originating in the posterior end of the worm is a capillary tube, equipped with flame cells, which runs anteriorly, dorsal to the enteron. In the cephalic region it dips ventral to the ganglion and turns abruptly to proceed posteriorly as a collecting duct differing from the capillary tube in size and in the absence of flame cells. It terminates at or near the posterior tip of the body. The tubes twist about each other throughout almost the entire length of the animal.

Reproduction is for the most part accomplished asexually by transverse fission. When a fission plane becomes sufficiently advanced, separation occurs and the two zooids, or chains of zooids, assume separate existences.

Sekara (1924) described sexually mature individuals. According to him, both the male and female gonads lie in the pseudocoel and are without extensive ducts or accessory apparatus. Marcus (1945a) describes both male and female gonads but differs with Sekara as to the position of the male gonad and its opening. According to Marcus the gonad is dorsal rather than ventral. The single ovum is located centrally in the post-intestinal region. This writer has never observed sexuality in any species, either in recently collected material or in cultures under constant observation for over fifteen years.

KEY TO THE AMERICAN SPECIES OF CATENULA

1. (a) Length of the cephalic region less than twice its width (fig. 4, F) 2
   (b) Length of the cephalic region more than twice its width (fig. 4, D and G) 4
2. (a) Cephalic region approximately ½ the length of the first zooid (fig. 4, F); chain 4-8 or more zooids; form balustrade (fig. 4, B) (Plate I) ....*lemnae*
   (b) Cephalic region less than ½ the length of the first zooid (fig. 4, C and E); chain usually of 1-8 zooids; form not balustrade (fig. 4, A) 3
3. (a) With a dorsal, ciliated groove on pre-oral zone (Plate III, D) ....*virginia*
   (b) Without dorsal, ciliated groove on pre-oral zone (fig. 4, E) (Plate II, A and B) ....*confusa*
4. (a) Cephalic region elongated anteriorly into a point, cephalic lobes located immediately anterior to the pre-oral groove (fig. 4 D) (Plate II, C and D)............*leptocephala*
   (b) Cephalic region rounded anteriorly, lobes located midway in the cephalic region (fig. 4, G) (Plate III, A and B) ....*sekerai*



Figs. 1-4.—A. Diagrammatic, dorsal, optical view of a *Catenula*. B. Lateral view of same. *cg*, cephalic ganglion; *e*, enteric cavity; *ee*, enteric epithelium; *ep*, excretory pore; *pn*, protonephridium; *ps*, pseudocoel; *s*, sphincter; *st*, statocyst; *epi*, epidermis; *m*, mouth; *ph*, pharynx; *pg*, pre-oral groove. 2. Statocysts from fixed material of *C. lemnae*. 3. Statocysts from living specimens of *C. leptocephala*. 4. A. Non-balustrade form. B. Balustrade form. C. Outline of *C. virginia*. D. *C. leptocephala*. E. *C. confusa*. F. *C. lemnae*. G. *C. sekerai*.

CATENULA LEMNAE Dugés
Plate I

The review of a large number of papers, many of them referred to later, has convinced the author that the name *C. lemnae* has been used in an almost generic sense for any *Catenula*, and, in most cases since 1832 has it been applied to other species than that described by Dugés. The species which has

been most commonly confused with *C. lemnae* is sharply defined and is widely distributed in the eastern United States and appears also to occur in Europe. This species is described in this paper under the name *C. confusa*.

C. lemnae has been collected several times from ponds in the vicinity of Augusta, Georgia, and once from Valdosta, Georgia.

The specimens vary greatly in length, depending upon the number of zooids in the chain and the state of nutrition of the worm. Chains of four to eight zooids are usual, and in one case forty-nine zooids were observed in a chain. Long chains of zooids are extremely threadlike in appearance. Length ranges from 1.5 to 16 mm. Contracted specimens have almost twice the width of extended ones.

The cephalic region of the anterior zooid is marked off posteriorly by a sharply defined pre-oral groove. Behind the first zooid, the cephalic region in each succeeding well-developed zooid of the chain is delimited both anteriorly and posteriorly by a sharply pronounced constriction. Each cephalic zone is somewhat less than twice as long as wide. These deep constrictions give the animal a rugose appearance when the worm is contracted (Plate I, D.).

In reflected light the organism is milky white in color. In transmitted light the body wall, pseudocoel, and cephalic end are light gray to brown. The enteric tract is generally slightly darker and in well fed specimens the dilated portion of the enteron in each zooid appears almost black.

The general ciliary coat is fine (cilia, approximately .012 mm long), except for the cilia around and in front of the pre-oral groove, which appears longer, denser and heavier. The cilia at the posterior end of the last zooid are extremely prominent. They are about four times as long as the epidermis is thick, and are generally kept at rest, whereas the cilia elsewhere are always in motion. The epidermis measures about .003 mm in thickness.

The cephalic ganglion appears as an elongate mass in the anterior end of each zooid. The mass seems to be constricted transversely near the middle. From this constriction it narrows anteriorly. The posterior part broadens, giving rise to at least one posteriorly directed cord on each side. The spherical statocyst lies partly embedded on the postero-dorsal region of the ganglionic mass.

There is considerable variation in the diameters of both the vesicle and the statolith—.01 to .02 mm for the vesicle and .008 to .016 mm for the statolith.

When the animal is at rest, the anterior lip of the narrow, V-shaped mouth is covered by the posterior fold of the cephalic region. The lips are heavily muscled and their margins are elaborately ciliated. The mouth opens into a muscular, short, tubular pharynx the inner lining of which is heavily ciliated. Posteriorly the pharynx opens through a sphincter into the wide enteron, which narrows sharply before it reaches the posterior end of each zooid. The enteric epithelium is finely ciliated.

The pseudocoel is traversed by numerous radial muscle fibers. It is tightly filled with cells of various sizes and shapes, except for a cell-free vesicular region in the end of the last zooid.

The protonephridial system is similar to that described for the genus as a whole.

C. lemnae has been successfully cultured for several years in wheat grain infusions.

Special diagnosis.—Rugose and balustrade in appearance, width of cephalic region approximately one-half the length; cephalic region approximately one-half the length of the first zooid; protonephridium not readily obvious; large in size; chains of from 1 to 49 zooids have been observed.

Catenula confusa n. sp.
Plate II, A and B

This species has been collected from ponds and roadside ditches throughout the eastern United States. It is the most common of all species of *Catenula* collected.

Single zooid specimens range from .354 to .5 mm in length; eight zooid specimens, 3.2 mm; extended worms measure from .083 to .091 mm in width. Chains of two to four zooids are of most frequent occurrence.

The general form is thread-like; the anterior end is rounded and the posterior end tapers into a blunt point. A deep pre-oral groove separates the cephalic region from the rest of the zooid. Developing fission planes of the more mature zooids form prominent constrictions at intervals in a chain. The ratio of the length of the cephalic region to the total length of the zooid in a single zooid specimen is about 1:5; in a two zooid specimen the ratio of the anterior zooid's cephalic region to the chain becomes approximately 1:8. Anteriorly the cephalic region is rounded; posteriorly it is symmetrically expanded into lateral lobes.

In reflected light the worm is milky white in appearance. Greenish granules are scattered throughout the parenchyma.

The cilia of the general ciliary coat measure about .01 mm in length. In the region of the pre-oral groove the cilia are thicker and longer.

The cephalic ganglion conforms to the general shape of the head. It is prolonged anteriorly into a point, but widens considerably between the lateral cephalic lobes. Embedded dorsally in the tissue of the posterior part of the ganglion is the statocyst which measures from .016 to .018 mm in diameter in mature zooids. The statoliths vary in diameter from .004 to .006 mm.

The V-shaped mouth is situated ventro-posteriorly to the pre-oral groove. It is bounded by muscular, heavily ciliated lips and opens into a short, muscular, ciliated pharynx. The pharynx opens through a sphincter into the ciliated enteron. In the mid-region of each zooid the enteron is distinctly widened, and as it approaches the posterior end of the zooid it narrows gradually.

Irregularly shaped cells fill the pseudocoel. Muscle strands traverse the pseudocoel in all regions of the body, and are particularly prominent at the anterior and posterior ends of the body. In contracted specimens the parenchymatous cells appear to be organized into irregular rolls.

The protonephridial system follows the generic pattern. The nephridiopore opens at the posterior end of the body.

This species does not culture under laboratory conditions.

Specific diagnosis.—Anterior cephalic region bluntly rounded; cephalic auricles at posterior end of cephalic region; cephalic region distinctly less than one-half the length of the body of a mature zooid; 1-8 zooids; statocyst embedded in postero-dorsal aspect of ganglion.

CATENULA VIRGINIA Kepner and Carter
Plate III, D and E

It has been impossible to obtain living specimens of *C. virginia* for study. The following is from the original description of Kepner and Carter (1930) and from a subsequent paper on this species by Heinlein and Wachowski (1944). *C. virginia* was collected by these authors from a stream near Scottsville, Virginia, and from Washington, D. C. The quotations used in the description are from Kepner and Carter (1930).

The spindle-shaped body of a single-zooid specimen measures about 0.5 mm; that of two zooid specimens, 1.0 mm. A chain of more than two zooids was not observed. The cephalic region is separated sharply from the body proper by a distinct pre-oral groove.

The epidermis is composed of low epithelium uniformly ciliated except for that of the oral region where the cilia are longer than those of the general body surface. The mesoderm is differentiated into an axial, coarsely granular region and a region presenting larger radiating vacuoles.

The T-shaped mouth lying on the ventral side immediately posterior to the transverse groove opens into a highly ciliated pharynx. "The pharynx opens into a sac-shaped, straw-colored enteron which may be seen projecting as ridges through the axial, granular mesenchyme."

The most conspicuous feature of the cephalic lobe is a statocyst which lies within the radial mesenchyme dorsal to the mass of axial, granular mesenchyme. On the dorsal surface of the cephalic lobe a pit extends posteriorly along the mid-dorsal line from the tip of the lobe to a little beyond its middle. The statocyst and the dorsal pit both have intimate connection with the dorsal ganglion.

"The statocyst does not lie dorsal to the cephalic ganglion as is given for its position in other species, but lies against the posterior vertical wall of the cephalic ganglion." As pointed out previously in this paper, Marcus states that this is the only position in which the statocyst is found in *Catenula*. "The wall of the statocyst is composed of an endothelium the cells of which are quite small. The statolith in life appears as an highly refractive homogeneous body; but in fixed material it appears to be a minute cell with a small amount of cytoplasm surrounding a nucleus. Within the nucleus of the statolith cell a nucleolus lies.

The median dorsal pit is lined with a modified region of the general epidermal epithelium. The cilia of this region are not much larger than those found over the general surface of the cephalic lobe or 'head.' The epithelium of the dorsal pit occupies about one-third of the dorsal width of the cephalic lobe at the region in which it lies. The general epithelium of the dorsal pit is a simple, low columnar one, except at the point where it stands in connection with the anterior nerve of the cephalic ganglion. At this point it tends to become stratified and lacks a well-defined basement membrane. Into this area, in which several layers of nuclei are found, an anterior median nerve is sent from the brain."

The protonephridium is similar to that described for the genus as a whole.

Specific diagnosis.—Not more than 2 zooids; dorsal cephalic pit present; body about .5 mm long.

Catenula leptocephala n. sp.
Plate II, C and D

This species was collected only from a small, permanent pond in the vicinity of Athens, Georgia. The total length and general size of specimens of this species vary greatly and is dependent upon nutritional state, age of zooids, and number of zooids in a chain. The usual number of zooids is two; but chains of three are not uncommon and of four are occasional. Single zooids measure .4 to .5 mm in length and .03 to 0.5 mm in width, two-zooid specimens, .5 to .7 mm in length and .03 to .06 mm in width. In extended three-zooid chains the ratio of width to length is about 1:30.

The body tapers both anteriorly and posteriorly. The cephalic region, which is about one-sixth the total zooid length, is prolonged anteriorly into a tapering snout which is about two-thirds the entire cephalic region in length. The posterior one-third of the cephalic region is expanded laterally into distinct lobes or auricles.

In reflected light the animal is milky white; in transmitted light the enteron is yellowish to brown and the parenchyma, greenish or yellowish.

Cilia of the general ciliary coat measure from .008 to .01 mm and are about four times the thickness of the epidermis. In the pharyngeal region the cilia are thicker, stouter, and longer than those in other regions of the body. With the exception of the cilia at the end of the last zooid, the cilia appear to be in almost constant motion.

Conforming to the general shape of the head, the cephalic ganglion is roughly triangular with its greatest width in the region of the posterior lateral expansions. Anteriorly it is prolonged into a tapering point extending about three-fourths the length of the cephalic region.

Embedded dorsally in the tissue of the ganglion at the point of greatest width is the refractive statocyst measuring from .008 to .01 mm in diameter. This structure carries a statolith measuring approximately .004 mm.

The V-shaped mouth lies just posterior to the ciliated pre-oral groove. The lips are well muscled and heavily ciliated with the anterior lip somewhat concealed by the posterior head margin. The mouth opens into a muscular, ciliated, tubular pharynx. At its posterior end the pharynx opens by a sphincter into the wide sac-like enteron which almost completely fills the space within the body wall. The enteron extends almost to the end of the zooid and conforms to the tapering shape of the body.

The cells of the pseudocoel are of various sizes and shapes and their cytoplasm appears fairly granular. Transverse muscular bands are not apparent.

The prominent protonephridial system conforms to the general pattern for the genus (fig. I) . The protonephridial pore is located at the posterior end of the last zooid.

Special diagnosis.—Rarely more than 1 mm in length; cephalic region elongated anteriorly into a point; cephalic auricles located just anterior to the pre-oral groove; cephalic region approximately one-fourth to one-eighth the length of the anterior zooid; pseudocoel in region of enteron fairly narrow; protonephridium easily observed; chains of more than four zooids unknown.

CATENULA SEKERAI Beauchamp
Plate III, A, B, C

This species was collected in large numbers on several occasions over a period of two years from a clear, cool pond located seven miles south of Valdosta, Georgia.

There can be little doubt that the species described here is identical with *C. sekerai* Beauchamp. It has two unique features exhibited by *C. sekerai*, namely, lateral lobes in the middle of the cephalic region and a statocyst located far anterior to its usual position in the genus. Although Beauchamp's description is none too extensive, comparison of other features also support this diagnosis of specific identity.

Measurements show the specimens to average .55 mm in length. Maximum observed length of a two zooid specimen was approximately .95 mm. In diameter the range is from .04 to .055 mm. Chains of more than two zooids have not been observed.

In general the body is cylindrical and somewhat flattened ventrally. Viewed dorsally the worm shows slight tapering from the pharyngeal region forward to the bluntly rounded anterior end. The posterior one-third of the body tapers sharply to terminate as a rounded point.

The cephalic region is distinctly marked off from the rest of the body by a deep pre-oral groove. The anterior two-fifths of this region is dorso-ventrally compressed and is somewhat spatulate in appearance. The middle one-fifth is distinctly dilated laterally and ventrally. The posterior two-fifths is narrowed anteriorly but gradually increases in diameter as it proceeds posteriorly.

About midway in the pharyngeal region there are pronounced constrictions in the lateral body wall.

In reflected light the animals are milky white, but in transmitted light the epidermis, pharyngeal, and cephalic regions are translucent and brownish in color. The depth of color of the enteric region is largely dependent on the food content and is generally of a darker brown color.

The general ciliary coat is uniform, prominent, and the ciliary length is about two and one-half times the epidermal thickness. The cilia on the anterior and posterior borders of the pre-oral groove are stout and long. The epidermis is rather thin, measuring .0033 mm in thickness.

The cephalic ganglion is roughly diamond shaped with the greatest width occurring about midway of the cephalic region between the median cephalic dilations. The anterior apex extends well forward; the posterior apex terminates near the pre-oral groove.

The statocyst lies embedded in the dorsal side of the ganglion along the midline in the region of the greatest ganglionic width. The statocyst's vesicle averages about .01 mm in diameter; the centrally located statolith, approximately .004 to .005 mm.

There appear to be two pairs of small latero-dorsal ciliated depressions: an anterior pair just in front of the median cephalic dilation and the posterior pair immediately behind this dilation. This species fixed so poorly that details of the cephalic region could not be satisfactorily studied.

The anterior margin of the V-shaped mouth is located on the midventral line just posterior to the pre-oral groove. The lips are well muscled and bear

on their exposed surfaces extremely long and stout cilia. Similar cilia are also apparent on the ventral and lateral margins of the pre-oral groove. The mouth opens into a ciliated, tubular pharynx which is deeply constricted in the mid-region. The original description calls for glands throughout the length of the pharynx and cells which may well be glandular were observed in this region.

Posteriorly the pharynx opens through a sphincter into the enteric tube. This tube conforms to the general shape of the posterior end of the body and extends almost to the end and in a single-zooid specimen. The enteric epithelium is composed of large cells, but the enteric lumen is relatively wide and is continuous throughout most of the length of the enteron.

Even though there is little pseudocoelic space, in both the pharyngeal and cephalic regions the pseudocoel contains many large, finely granular cells. Traversing the pseudocoel at various points may be seen evidence of the radial musculature.

The protonephridial system conforms to the common pattern for the genus.

Specific diagnosis.—Pseudocoel in region of enteron distinctly narrow; lobes or dilations located midway in the cephalic region; cephalic ganglion roughly diamond-shaped; two pairs of cephalic, latero-dorsal depressions which resemble ciliated pits, statocyst located near center of cephalic region.

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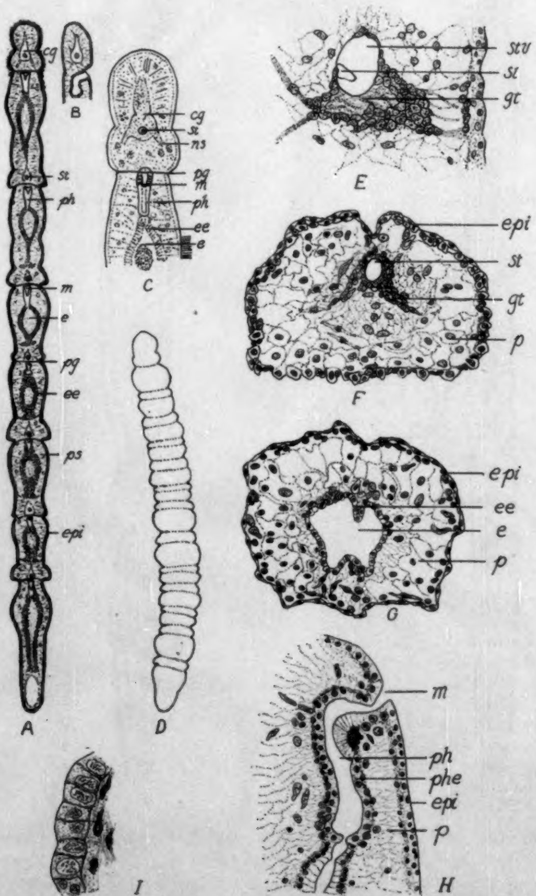
ABBREVIATIONS FOR PLATES

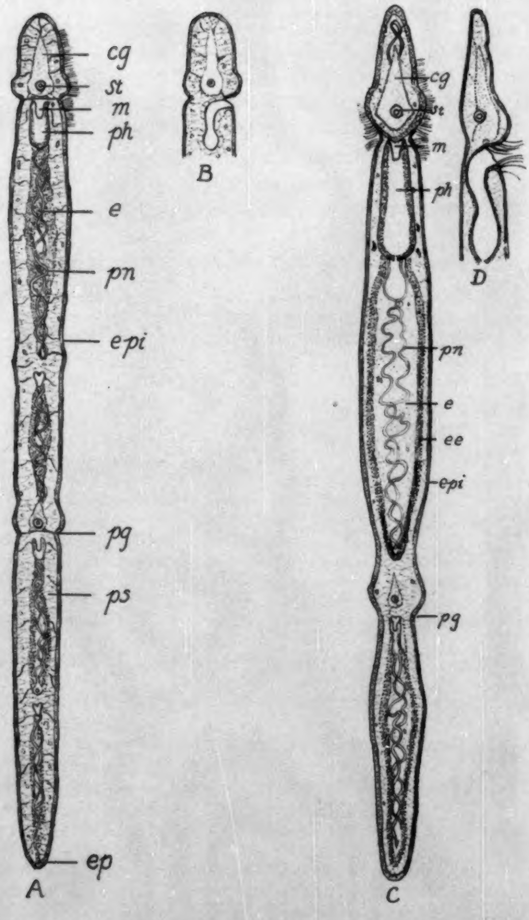
c, region in epithelium of floor of dorsal pit; cg, cephalic ganglion; cp, ciliated pit; dp, dorsal pit; e, enteric cavity; ee, enteric epithelium; en, enteron; ep, excretory pore; epi, epidermis; gm, granular, axial mesenchyme; gt, ganglionic tissue; m, mouth; ns, nerve stem; p, parenchyma; pg, pre-oral groove; ph, pharynx; phe, pharyngeal epithelium; pn, protonephridium; ps, pseudocoel; rm, radial mesenchyme; s, sphincter; sl, statolith; st, statocyst; stv, statocyst vesicle; tg, transverse, pre-oral groove.

PLATE I



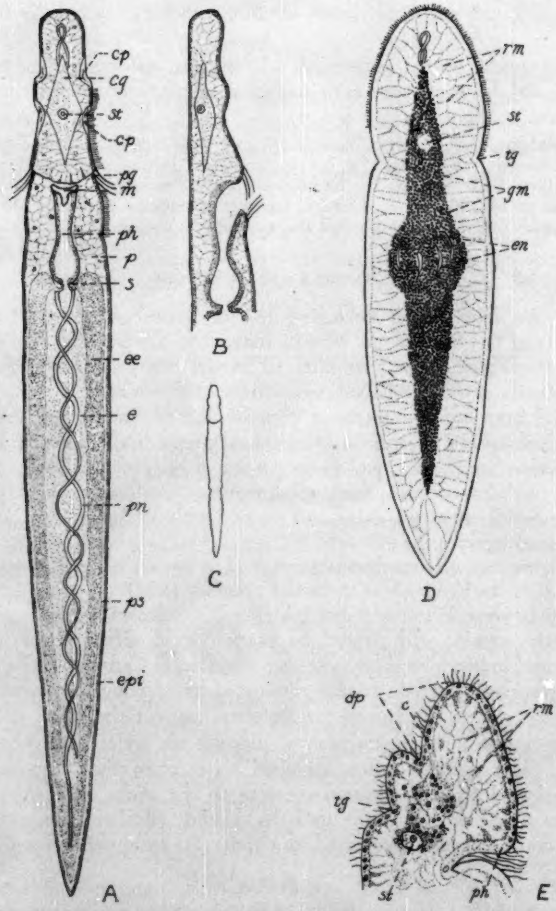
A. Dorsal view of *C. lemnae*. B. Lateral aspect of cephalic and pharyngeal regions. C. Enlarged cephalic region. D. Outline of a contracted specimen. E. Longitudinal section through cephalic ganglion. G. Cross section through enteron. H. Longitudinal section through the pharynx. I. Portion of the epidermis showing the longitudinal musculature.

PLATE II



A. Dorsal view of *C. confusa*. B. Lateral aspect of cephalic and pharyngeal regions. C. Dorsal view of *C. leptocephala*. D. Lateral aspect of cephalic and pharyngeal regions.

PLATE III



A. Dorsal view of *C. sekerai.* B. Lateral aspect of cephalic and pharyngeal regions. C. Outline of two zooid specimen. D. Dorsal view of *C. virginia* (redrawn from Kepner and Carter, 1930). E. Sagittal section through axis of cephalic lobe (redrawn from Kepner and Carter, 1930).

Intestinal Parasitism of Some Mid-Western Salamanders[1]

Thomas D. Malewitz[2]

In this study several genera of salamanders collected from Oklahoma, Arkansas, and Missouri were examined to determine the incidence and species of endoparasites.

Acknowledgment.—The author is indebted to Miss Mary E. Larson, Department of Zoology, University of Kansas, for her guidance and helpful suggestions; to Professor A. C. Walton, Knox College, for identification of the nematodes from *Cryptobranchus bishopi;* and to Mr. Harold A. Dundee, formerly a graduate student at the University of Kansas, who collected and identified the salamanders used in this project.

Materials and Methods

Thirty-five salamanders belonging to the genera *Eurycea, Ambystoma, Plethodon* and *Cryptobranchus* were dissected and the parasites recovered were placed in amphibian Ringer's solution (Thomas, 1950) for observation. Parasites found were acanthocephalans, trematodes, and protozoans.

Material from four specimens of *Cryptobranchus bishopi* was scraped from several loci along the intestine, and examined methodically for ova and protozoan parasites. Seven examinations were made of each of the four samples.

Blood, withdrawn from three specimens of *Cryptobranchus bishopi,* was placed on a slide, smeared, dried and stained with Wright's stain. All blood examined was negative for parasites.

Whole mounts of acanthocephalans and trematodes were prepared by a modification of the Pereira-Vaz method (Thomas, 1950).

Nematoda were killed and fixed in Bouin's solution, stained with Semichon's acetic carmine, dehydrated by placing in a differentiator (Thomas, 1950), cleared in beechwood creosote and mounted in Canada balsam. The use of the differentiator for dehydration eliminated transferring specimens and thus decreased the chance of damage to the parasites (in the usual dehydration method specimens must be transferred through six series of alcohol, 70-100 per cent). The parasites often absorbed water from the atmosphere when being transferred from beechwood creosote to the slide. Therefore, Canada balsam was added drop by drop until the clearing solution became thick. The specimens could then be transferred to a slide and mounted without absorbing water.

Observations

Acanthocephalans.—Acanthocephalus van-cleavei Hughes and Moore, 1943 was recovered from eight of nineteen specimens of *Eurycea multiplicata* collected from Cherokee County, eight miles north of Tahlequah (McSpad-

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[1] Submitted to the University of Kansas in partial fulfillment of the requirements for the degree of Master of Arts.

[2] Present address: Department of Anatomy, Michigan State University, East Lansing.

den Falls), Oklahoma on May 11, 1952. The parasites were present in the intestine about 12 mm posterior to the stomach. They are being assigned tentatively to *A. van-cleavei* on the basis of the arrangements of the hooks on the proboscis.

Only three species of *Acanthocephalus* (*A. ranae, A. acutulus* and *A. van-cleavei*) have been reported from North American Amphibia (Hughes and Moore, 1943; Ward, 1951, 1952).

Trematoda.—Small, gray white immature trematodes were recovered from the intestine of a single specimen of *Ambystoma opacum* obtained on January 27, 1952, in Choctaw County, two miles east of Swink, Oklahoma.

Because of the presence of a poorly defined oral sucker and the absence of recognizable internal structures, no description or classification of this parasite was attempted.

Spironoura wardi Mackin, 1936 and *S. variabilis* (= *Zanclophorus variabilis*), Walton, 1936—These species were recovered from five specimens of *Cryptobranchus bishopi* collected in Spring River at Mammoth Spring, Fulton County, Arkansas on August 17, 1952 and October 26, 1952. Immature forms of *Spironoura*, sexes indeterminate, were judged to be *S. variabilis* because of the morphology of the lips. The parasites were numerous and were present in the small intestine in a region extending from 8 mm posterior to the stomach to 5 mm anterior to the anus.

Spironoura variabilis was described by Walton (1936) from *Cryptobranchus alleganiensis*. Mackin (1936) described *Spironoura wardi* from the intestine of the snapping turtle, *Chelydra serpentina*.

Measurements of *S. variabilis* and *S. wardi* were slightly larger than those stated by Walton (1936) and Mackin (1936). This difference in size may be due to their presence in *Cryptobranchus bishopi*, which is a newly reported host for these nematodes.

Fecal examination.—Fecal material from four specimens of *Cryptobranchus bishopi* was examined to determine if nematode ova could be recovered, however, none were found. All four salamanders were heavily parasitized with nematodes; seventy-five percent of the female nematodes recovered were mature and contained intrauterine ova. The absence of ova from the feces may possibly be correlated with the life cycle, which is not known, of these spironouras. Perhaps the ova may be extruded into the intestinal tract during a certain season of the year. The presence of immature *Spironoura* in the intestine suggests the possibility of intrauterine hatching of the ova. The life cycle of the nematodes may also be correlated with the life cycle of *C. bishopi*.

Protozoans.—An intestinal flagellate was found in the feces of *Cryptobranchus bishopi*. This species, which is oval to spindle-shaped, possesses three active anterior flagella, an undulating membrane which extended the entire length of the body and an axostyle. Rankin (1937) observed the presence of *Trichomonas augusta* in *Cryptobranchus*. Jahn (1949) characterized *T. augusta* in the genus *Tritrichomonas* on the basis of the presence of three anterior flagella. As a result of the observations, it was assumed that these intestinal flagellates belong to the Trichomonadidae Wenyon and either to the genus *Trichomonas* or *Tritrichomonas*.

SUMMARY

Salamanders of the genera *Eurycea, Ambystoma, Plethodon* and *Cryptobranchus* collected from Oklahoma, Arkansas and Missouri, were examined for intestinal parasites.

The feces from *Cryptobranchus bishopi* were examined for the presence of nematode ova, however, none were found. Flagellates of the family Trichomonadidae were present.

Immature trematodes were present in *Ambystoma opacum*. *Acanthocephalus van-cleavei* were present in *Eurycea multiplicata*. In *Cryptobranchus bishopi* the two nematodes, *Spironoura variabilis* and *S. wardi* were numerous in the intestine. This is the first report of *S. variabilis* and *S. wardi* in *C. bishopi*. This is also the first report of *S. wardi* in amphibians.

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On Sporangiostrobus Langfordi sp. nov., a New Fossil Lycopod Cone from Illinois

W. G. Chaloner[1]
University of Reading, England

The cone described in this paper is based on a single specimen consisting of part and counterpart of a Mazon Creek type of nodule (fig. 1) collected from one of the spoil heaps in the vicinity of Coal City, and now contained in the Langford Collection of the Illinois State Museum, Springfield. The specimen consists of about five centimeters of what was presumably at one time a much longer cone. It is preserved in the form of a compression, with little of the organic matter of the cone itself remaining as a carbonaceous film; but the positions of the sporangia in the flattened cone are represented by compressed masses of the thick-walled relatively resistant spores which they contained. These may be removed from the surface of the cone, macerated with Schulze's Solution (nitric acid with potassium chlorate) and examined microscopically (figs. 2 and 3). After treatment with Schulze's Solution the megaspores were placed in dilute alkali (ammonia solution) where the aggregated masses separated into the component spores. Some of these were mounted dry, and examined by reflected light; others were still further macerated and mounted as transparent objects in Diaphane for examination by transmitted light (Arnold 1950).

The genus *Sporangiostrobus* was founded by Bode (1928) on two species of microspore-bearing cones from Silesia. Bode did not consider the evidence of his specimens (which were rather poorly preserved) to indicate a lycopod affinity, and so deliberately gave them a name carrying no implication of any particular plant group. Nemejc (1931) described new material of the genus, including some megaspore-bearing cones, and transferred to Bode's genus two cones previously described by Feistmantel as *Sigillariostrobus*. He established that *Sporangiostrobus* was a lycopod cone on the grounds of the axillary position of the sporangium (borne at the base of the linear sporophyll) and the heterosporous condition of the cone. Its parent plant is unknown, but from its size it is reasonable to suppose that it may have been borne by an aborescent lycopod similar to *Lepidodendron* or *Sigillaria*.

The species of *Sporangiostrobus* at present known are therefore:

S. orzeschensis Bode 1928 (Microspore-bearing). From Orzesche, Silesia, Germany.

S. rugosus Bode 1928. (Microspore-bearing). From Orzesche, Silesia, Germany.

S. feistmanteli (Feistmantel 1876) Nemejc 1931. (Megaspore-bearing and ? hermaphrodite: see Nemejec l.c. p. 10). From two localities near Prague, Czechoslovakia (Nemejc) and South Limburg, Holland (Jongmans 1926 p. 1157).

S. cordai (Feistmantel 1876) Nemejc 1931. (Megaspore-bearing). From Czechoslovakia.

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[1] I should like to acknowledge the kindness of Dr. C. Condit who arranged for me to borrow the specimen described in this paper, and my indebtedness to the Commonwealth Fund from which I was in receipt of a grant during the course of this work.

Three of the four previously described species therefore all come from Eastern Europe in the vicinity of Czechoslovakia; the fourth is known both from the same area, and from Holland.

SPORANGIOSTROBUS Bode 1928

Diagnosis.—Large cylindrical cone, consisting of an axis of more than half the total diameter of the cone, bearing long linear spirally arranged sporophylls, in the axils of which sporangia are borne. Sporangia more or less circular in section tangential to the cone, with their radial length less than twice the height; containing either tri-radiate

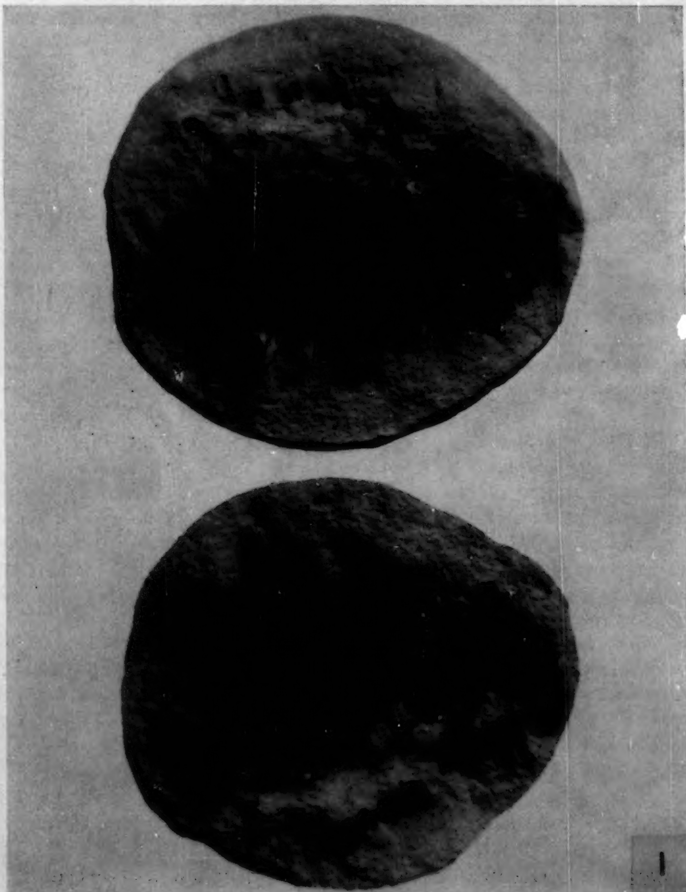

Fig. 1.—Holotype of *Sporangiostrobus langfordi* sp. n., ×1. Part and counterpart, in a Mazon Creek nodule from the vicinity of Coal City. The apex is to the left, the truncated base to the right. The sporangia are flattened endwise-on against the cone axis in the center of the cone, and are seen in side view along either margin. Specimen number 15560, Langford Collection, Illinois State Museum, Springfield.

microspores, or megaspores with an equatorial flange (i.e. of the Zonales section of *Triletes*). The cone may be composed of megasporophylls to the apex, or of megasporophylls below and microsporophylls above.

Genotype.—*Sporangiostrobus orzeschensis* Bode 1928.

Sporangiostrobus langfordi sp. n.
Fig 1

Diagnosis.—Cone of unknown length, at least 6 cm long and 4.5 cm wide, tapering rather abruptly at the apex. Axis forming about 3/5 of the cone diameter, 2.8 cm at the widest part. Sporangia 5-6 mm wide (measured tangentially to the cone), 5-6 mm high (measured parallel to the cone axis), up to 10 mm long (measured radially to the cone axis) with a rounded-truncate distal end. Apparently borne on the axis in the axils of the bracts, in alternating whorls (or in a spiral arrangement in which the two parastichies appear to be equally inclined to the axis). Sporangia containing only megaspores, agreeing with *Triletes superbus* Bartlett. Body of the megaspore spheroidal, 1740-2230μ in diameter (mean of 8 measured, 1970μ), with a broad equatorial flange formed by anastomosing outgrowths, 610-920μ wide, broadest opposite the triradiate ridges. Spore-wall 50-55μ thick. Hair-like outgrowths 10-15μ wide distributed over the spore body, concentrated mainly in the equatorial region, where they merge with the flange, diminishing in length and density towards the distal pole; absent or rare on the contact faces. Triradiate ridges relatively tall (up to 760μ high) with vertical plications and striae, extending to the equator of the spore body.

Holotype.—(fig. 1) From the vicinity of Mazon Creek, Illinois. Presumably from the shale above the No. 2 Coal, Carbondale formation, Pennsylvanian. Part and counterpart, No. 15560, Langford Collection, Illinois State Museum, Springfield, Illinois.

DISCUSSION

Nemejc (1931) gives details of only one species of megaspore-bearing cone (*Sporangiostrobus feistmanteli*) and figures the megaspores. The existing figures of the only other megaspore-bearing species are inadequate for any detailed comparison and no description or figures of its megaspores are available. The only species with which any comparison of *Sporangiostrobus langfordi* sp. n. can be effected is therefore *S. feistmanteli.* This differs from the Illinois specimen in that it appears from Nemejc's figures 4 and 4a (loc. cit.) that the sporangia are of more or less equal dimensions in all directions, and have no appreciable radial elongation (as in *S. langfordi*). In other lycopod cone genera (e.g. *Lepidostrobus*) the ratio of sporangium length to breadth is a rather constant feature within a species. I therefore regard this as a valid distinction between these two species.

Fig. 2.—Part of a megaspore from the above cone, photographed by transmitted light to show detail of the reticulate structure of the marginal flange. ×25.

From Nemejc's figures the megaspores that he obtained from *Sporangiostrobus feistmanteli,* it appears that the flange or wing around the spore was composed of more or less discrete, spoke-like projections, fusing at the periphery

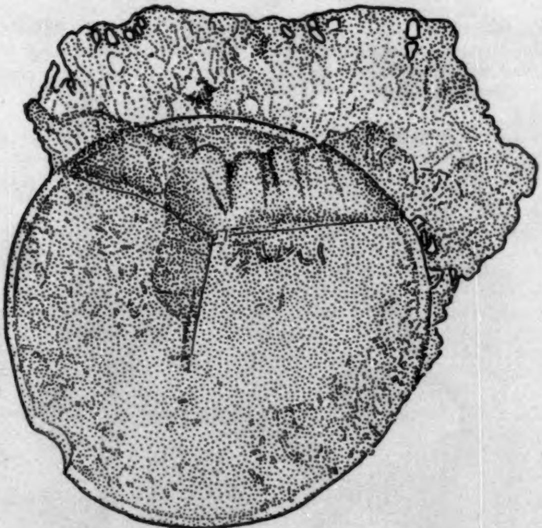

Fig. 3.—A damaged megaspore (of the *Triletes superbus* type) from the holotype of *Sporangiostrobus langfordi* sp. n., showing the structure of the marginal flange and the tall, plicate, triradiate ridges, ×25.

(Nemejc's plate figs. 1-3). It is not altogether clear from these figures whether Nemejc's spores agree most closely with *Triletes superbus* Bartlett, or *T. rotatus* Bartlett. They appear to differ from the spores of *S. langfordi,* however, in the more continuous lace-like structure of the flange of the spores of the latter species (cf. figs. 2 and 3). I therefore regard *S. langfordi* as distinct from *S. feistmanteli* on the basis of both the sporangium shape and the megaspore structure.

Owing to the very fragile nature of the flange around the megaspores, I failed to obtain any megaspores from *S. langfordi* in which this was completely undamaged. From Nemejc's figures it appears that he encountered the same difficulty with the megaspores of *S. feistmanteli.*

No further evidence is contributed by the Illinois specimen to the nature of the sporophyll lamina in *Sporangiostrobus.* These linear leaf-like prolongations of the sporophyll were apparently lost during or before fossilization, in this specimen, as in Bode's and some of Nemejc's specimens. The tendency for the sporophyll lamina to be shed or to rot away seems to be particularly common in this genus. Specimens of *Lepidostrobus* are sometimes found in which the "cone" is composed only of the exposed sporangia, the distal part having been lost in a comparable manner. The original presence of a sporophyll in *S. langfordi* is merely surmised on the basis of the similarity of the material in all other respects with Nemejc's better-preserved material.

SPORANGIOSTROBUS AND SIGILLARIOSTROBUS

In a recent paper, Potonié (1954 p. 112) reverts to Feistmantel's name,

and again refers *Sporangiostrobus feistmanteli* to *Sigillariostrobus*. It seems desirable however, to maintain the distinction between these two genera, which was made by Bode and subsequently strengthened by Nemejc's work. As has been indicated elsewhere (Schopf 1941, Chaloner 1953) it is more satisfactory to reserve the genus *Sigillariostrobus* for those lycopod cones showing close similarity to those at present believed, on good grounds, to have been borne on *Sigillaria*. Those species for which connection with *Sigillaria* has been demonstrated, on the basis of both compression and petrifaction specimens, show certain distinctive features in common—viz., the cone is pedunculate, the megaspores are saucer-shaped (i.e. markedly flattened and more or less concavo-convex) and the cones are either male or female, never hermaphrodite (Schopf, Chaloner loc. cit.). The more important differences between *Sporangiostrobus* and *Sigillariostrobus* may be summarized as follows:

SPORANGIOSTROBUS	SIGILLARIOSTROBUS
Megaspore with a broad marginal flange; spore-body spheroidal (i.e. of the Zonales section of *Triletes*).	Megaspores lacking a marginal flange; spore body saucer-shaped (i.e. of the Mazospora section of *Triletes*).
Cone-axis at least half the total width of the cone.	Cone-axis considerably less than half the total width of the cone.
Sporophyll lamina relatively long, parallel-sided; readily shed, leaving the sporangium attached to the cone axis.	Sporophyll lamina relatively short, triangular, rarely detached from the remainder of the sporophyll.
Cone attachment unknown, probably terminal on a vegetative shoot (see Nemejc 1931 p. 11).	Cone pedunculate. Cones, borne on peduncles, in irregular zones on the main trunk of the tree.
Some cones known to be hermaphrodite.	No hermaphrodite cones known.

These two cone genera, if they are to have any useful meaning, must be distinguished on characters innate in their structure, and not on their supposed affinities. However, in addition to the distinctions just cited, it is relevant to note that while connection with *Sigillaria* has been inferred for a number of cones of the *Sigillariostrobus* type, the parent plant of *Sporangiostrobus* is still unknown. On the basis of the information at present available, as summarized in the table above, it seems justifiable to maintain these two genera, which appear to be reasonably natural and distinct groups of cones.

DISTRIBUTION OF SPORANGIOSTROBUS

Megaspores (*Triletes superbus* Bartlett) agreeing with those obtained from *Sporangiostrobus langfordi* were first recorded from pebbles of coal occurring in the glacial drift at Ann Arbor, Michigan, by Bartlett in 1929. They were in fact the most abundant of the several species occurring in the pebbles. Since then, very similar spores have been recorded from many localities: from Holland, Belgium, France, Germany and Scotland (Dijkstra 1946), from Turkey (Dijkstra 1952), from Czechoslovakia (Kalibova 1951), and from West Virginia (Cross 1947). I have also found them in great abundance in some coals of the Farrington Series from Somerset, England (of Radstockian age, i.e., high Pennsylvanian). Dijkstra (1953) gives the vertical distribution of this megaspore (based on the data given in all these published records) as Westphalian B-D. In view of this widespread occurrence of these megaspores and of their great abundance at certain horizons, it is rather surprising

that the cones of *Sporangiostrobus* type which bore them, are so rare and of such local occurrence compared with *Sigillariostrobus* and *Lepidostrobus*. It is clearly possible that the plant which produced *Sporangiostrobus* was a component of an upland flora rather than that forming the vegetation of the coal swamp; and that the megaspores found in such quantities in coals were wind or water borne from some distance. Even so, it is surprising that there are not more extensive records of *Sporangiostrobus*. The discrepancy between the abundance of the spores of the *Triletes superbus* type and the rarity of *Sporangiostrobus* cones is perhaps merely symptomatic of the rather unrepresentative nature of the total Pennsylvanian flora, as it is represented by fossil plant compressions.

Summary

A new fossil lycopod cone, *Sporangiostrobus langfordi* sp. n. from a Mazon Creek type nodule is described. Its megaspores are identified with those previously described isolated from coal, as *Triletes superbus* Bartlett. The genus *Sporangiostrobus* Bode has hitherto been known only from the upper Carboniferous of central Europe. The several characters distinguishing *Sporangiostrobus* from *Sigillariostrobus* are listed and discussed.

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The Breeding Systems of Lupinus, Group Micranthi

David B. Dunn

Rancho Santa Ana Botanic Gardens, Claremont, California

Lupinus section *Micranthi* is a group that contains many small flowered annual lupines and ranges from British Columbia to northern Mexico. They have the characteristic flower of the Pea family, and like many, if not most, of its members are self pollinated to a large degree, because of the floral structure, the keel containing both the stamens and style in close proximity. While studying the taxonomy of this group and growing some of its members for purposes of comparison, it was observed that in the greenhouse flowers of *L. bicolor* regularly set seed, but that those of *L. nanus* failed to do so. Were it not for the self pollinating mechanism this might have been attributed to the absence of insects. Preliminary investigation indicated a difference in the way that this mechanism operates and hence a difference in the variation pattern of the two species. The purpose of this investigation is to ascertain and clarify these differences.

First the structure of the flower is carefully analyzed and thereafter follows a discussion of the insect relationship and how bees operate the pollination mechanism in *L. nanus*. Experiments designed to study the rate of floral development, the time of stigma receptivity, and the period of pollen viability are then presented and their bearing on selfing and outcrossing is discussed.

I am under obligation to Professor Carl Epling for advice and guidance.

Floral Structure

The flowers of Lupinus are borne in racemes and may be in whorls, in a spiral or simply scattered along the rachis. They may be erect, ascending, spreading or somewhat retrorse. The number in any raceme depends in part upon the species and in part upon the vigor of the individual.

The calyx is composed of five united sepals. The upper two are commonly joined below the middle. In most species the lower three are nearly or completely fused and are joined to the upper only near the base, thus forming a boat-shaped lip which lends support to the petals within.

The petals are typical of the Papilionoideae (Leguminosae). The banner at anthesis commonly has the upper half and sides reflexed. The lower unreflexed portion remains folded down over the upper edges of the other petals in such a way as to form a groove down the center, called the ventral median sulcus. This three way fold forms two umbos at the center and a sunken crease up the front reflexed portion of the banner. The umbos and the crease are commonly white and yellowish, with dark spots, surrounded by blue, a possible focal point of attraction for the insect. The crease and the sulcus form a continuous channel along which bees probe even though the lupines do not have nectar glands (Knuth, 1908).

Each wing is attached by a slender claw which bends readily. The rest of the petal is usually wide enough to cover the angled keel petals. The wings are generally fused toward the apex and sometimes above, behind the tip of the keel.

The petals of the keel are likewise attached by a slender claw which bends readily, and are fused firmly on the lower margin, from below the middle to the apex. They are also fused on the upper margin varying distances from the acumen. The tip of the acumen is left free to form a pore like opening. The lower margin of the keel forms a guiding trough gradually narrowed toward the tip of the acumen.

The stamens are monadelphous, five bearing larger anthers, alternating with five bearing smaller ones (fig. 1). In the bud the latter have shorter filaments which later elongate. The pollen of the five large anthers is shed into the keel while the flower is still unopened and forms a coherent mass surrounding the style. This pollen mass is forced upward into the acumen by elongation of the filaments of the still unopened small anthered stamens, which act as a piston guided by the fused margins of the keel. During this

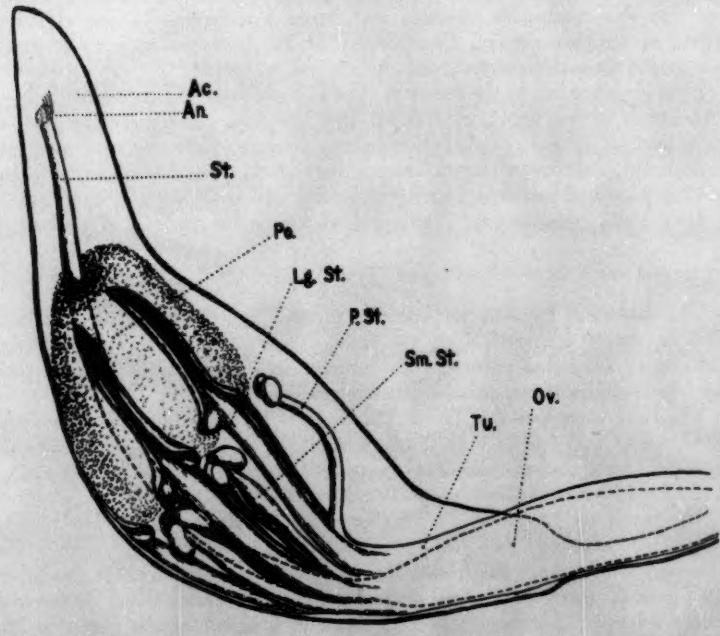

Fig. 1.—Keel, Stamens and Pistil of *L. nanus menkerae.*—The large stamens have shed their pollen and reached their maximum growth in length. Ac—Acumen into which the pollen mass is shoved. An—Stiff circle of hairs protecting the stigma. St—Style. Po—Pollen mass from the 5 large stamens. Lg St—Large stamen. Sm St—Small stamen. P St—Posterior small stamen. Tu—Stamen tube. Ov—Ovary. The keel ciliation has been omitted for clarity.

process the small anthers also open. As a result, the pollen mass is deposited around the stigma in the still unopened flower. The stigma, however, is shielded from it by a fringe of erect hairs. When this point has been reached, the banner reflexes and the flower is *open.* The acumen may now be likened to a cylinder filled with pollen, which is supported in place by 4 small-anthered stamens, and the style. The stigma, it will be remembered, is shielded by the erect fringe of hairs. The upper small-anthered stamen, not having a guide, bulges outward and withers after shedding its pollen. The flower is now ready for pollination.

Beyond this point the functioning of this mechanism differs according to the size of the flower. *L. bicolor* may be taken as an example of the smaller flowered forms, and *L. nanus* of the larger. The former appear to be obligatorily selfed, without the intervention of insects; the latter require the visit of an insect in order for pollination to take place at all. When it does it is apparently chiefly self pollination, but a means of outcrossing is also provided.

The flowers of *L. bicolor* are small, relative to those of *L. nanus* but the ranges of the two species are more or less continuous, some forms of *L. bicolor* approaching the size of some forms of *L. nanus.* Bearing in mind these intermediate forms which may provide exceptions, the following is true. The flowers of *L. bicolor* are pollinated before they open or within a few hours after opening, and some do not open at all. They are seldom visited by insects. Evidence suggests that the stigma becomes receptive in the bud. Furthermore the length of the hairy fringe which shields the stigma is correlated with flower size and in *L. bicolor* it is too short to prevent self pollination. Hence, as soon as the stigma becomes receptive it is automatically self pollinated and fertilization follows. No pressure such as that which would be supplied by an insect is needed to operate the piston and thus force the pollen onto the stigma.

On the other hand, the fringe of hairs which protects the stigma of *L. nanus* is large and dense and effectively prevents contact of its own pollen with the stigma, so long as the flower is undisturbed. However, if one applies a vigorous downward pressure to the top margin of the keel, thus simulating the visit of insects, the keel, (the cylinder containing the pollen mass) is forced to slide along the stamens and style, and acting as a piston, forces the pollen from the acumen and gives it an opportunity for attachment to the insect. Hence, provision is made in the larger flowered forms for outcrossing, which is apparently impossible or very infrequent in the smaller flowered forms. At the same time, the fringe of hairs flares out and thus permits the stigma to come into contact with its own pollen. Hence, the pod may be self pollinated if the stigma has become receptive, but not automatically as in the case of *L. bicolor.*

INSECT RELATIONSHIP

The structure of the flower described in detail above prevents insects other than bees from being effective in the process of pollination.

The insects which have been observed visiting lupines by myself and others (Knuth, 1908; Robertson, 1917; and Bouvier, 1904) may be placed in three

categories: 1) those destroying plant parts, 2) those feeding on pollen primarily, and 3) those collecting pollen for food and incidentally aiding in pollination.

Insects destroying plant parts include, grasshoppers and beetles of various kinds which might accidentally trip the piston mechanism while eating the next flower but they are certainly not effective agents in pollination. The larvae of parasitic flies and moths have been collected on the plants but neither the adult nor the larvae could effectively trip the piston mechanism.

Insects which are classed as feeding on pollen primarily are the thrips, syrphid flies and a small coleopteran which Epling believes to be the pollinating agent in *Linanthus Parryi*. The same coleopteran was observed by Epling and Dunn visiting the flowers of *Lupinus odoratus* but since it entered the keel from below it could not operate the piston mechanism and would be classed as a robber. The thrips which Shaw (1914) found to produce a 20.8% pollination in sugar beets, when other insects were excluded; were also found to be common visitors of the lupines. The thrips also entered the keel from near the claws and fed on the pollen mass from below. The tip of the keel is not open unless pollen is being forced out by the piston mechanism described above. The thrips is the only insect commonly visiting the small flowered members of the *Micranthi*. While it has been shown to act as a pollinating agent in sugar beets, the structure of the flower, the stigma enclosed in a mass of pollen of the same flower and the time of receptivity of the stigma all suggest that the thrips could not empty the pollen mass from below and crawl forward through the acumen of the flower, crossing the stigma enroute, to act as a pollinating agent prior to self-fertilization. Hence, it seems highly improbable that the thrips is likely to act as a pollinating agent in the small flowered lupines and selfing would seem inevitable.

Syrphid flies have been observed visiting lupines. Syrphid flies are well known as pollen eaters. Brown (1918) has recorded watching one of these flies carefully remove all of the pollen grains from two anthers and then remove the pollen grains from the stigma as well. All of the syrphid flies observed by the present writer landed on flowers without causing any wing or keel movement and could thus only pick up pollen spilled by bees or pollen naturally exuding from the tip of the keel due to growth of a pollinated pistil.

The insects which collect pollen and incidentally aid in pollination are the various species of bees. From my observations only bees are able to manipulate the piston mechanism of the lupine flower. The larger flowered species are frequented by bees while the smaller flowered species are seldom if ever visited. The larger flowered species require the aid of the bees for pollination while the smaller flowered species do not.

Agreement is general that bees are constant visitors. Knuth (1908), citing his own observations as well as those of Müller, Alfken, and Lowe, lists the following genera as visitors of lupine flowers in European gardens: *Andrean, Anthidium, Apis, Bombus, Megachile* and *Osmia*. Robertson (1917) studied insect visitors to papilionaceous flowers and tabulated the percentages of visits of bees vs. other insect visitors for both social and non-social flowers.

The present writer has observed numerous individuals of *Apis*, several

species of *Bombus,* and a number of small bees belonging to either *Megachile* or *Osmia,* during their visits to lupines.

The technique of visiting is similar for all those observed. Approaching a flower, the bee generally heads directly towards the white center of the banner and when about one-fourth inch above the flower wings, drops down onto them (individuals of *Apis* are often erratic). Because of its weight the bumble bee, in particular, gives the flower a sudden jolt. This jolt and pressure is important in pollination as will be shown later. Because of it, a stream of pollen is forced out of the acumen by the action of the piston mechanism. The bee then proceeds to scoop up the pollen and pack it into the pollen baskets as described in detail by Bouvier (1904). At the same time it probes down along the sulcus of the banner, its head pushing against the banner in many cases, thus actually giving more leverage for pressure on the flower wings and keel. Several strokes of pressure may be applied to the upper margin of the keel during one visit.

The acumen of the keel commonly passes to either side of the abdomen of *Apis* and may pass under the margin of a dorsal segment of the abdomen, one of the legs massaging the slender pollen filled acumen of the keel. The hairs on the abdominal segments become filled with pollen which is later transferred to the pollen sacks on the hind legs.

A choice of flowers is made, for only those verticils in which the flowers have reached a certain stage of anthesis are ordinarily visited. Since all the flowers in a verticil are approximately of the same age, all are usually visited systematically one after another. This choice is apparently governed by the white color spot of the banner, for the older flowers lower on the raceme, in which the color spot has turned to purple, are generally ignored. This change takes place within 24-48 hours following pollination. A relation therefore exists between the maturation of the flower and the insect visits.

The size of the flower, to a certain degree, governs the size of the bee necessary for effective pollination. Large flowers like those of *L. arboreus* and *L. excubitus* (14 to 18 mm long) require the visit of a large heavy bumble bee. In such flowers the banner is out of reach for smaller bees and cannot be utilized as a head prop for balancing. Hence, honey bees and other smaller species when visiting the flowers of *L. arboreus* have a difficult time to balance and apply leverage simultaneously. It is accordingly doubtful whether any but the occasional bumble bee is effective in the pollination of this species, a fact which may account for its poor seed set.

Lupinus nanus and its subspecies are frequented by nearly all of the bees observed. However, bumble bees frequently ignore this species when perennial lupines are nearby, even though their flowers are only slightly larger. The writer observed a bumble bee cross a dense *L. nanus* colony 100 ft. in diameter and go directly to a solitary perennial.

L. bicolor, on the other hand, is seldom visited by bees. In six years of observation I have seen only one small wild bee *(Megachile?)* visiting this species. This was in an experimental planting in the San Fernando Valley.

While the bees are able and effective carriers of pollen and often visit two or more taxa more or less indiscriminately, a self preference in pollination

in the flowers, demonstrated below for several taxa, the size of the flower for the size of bee and timing of visit of the bee may only be required to self the flower. A rough measure is as follows for the *Micranthi* and some large flowered perennials; flowers 8 mm long or less do not require aid and are seldom visited; flowers 10 mm long may or may not require aid and may be visited frequently or rarely by *Apis* (*L. bicolor* rare visit and *L. vallicola* requires visits); flowers 12 mm or larger are visited commonly by *Apis* and *Bombus* but for flowers above 14 mm in size it is doubtful whether *Apis* is effective.

Nevertheless, Burlingame (1921) found a solitary white flowered *L. nanus latifolius* (recessive) in a colony of blue flowered plants of the same taxon and was able to obtain seed. The seed produced both white and blue flowered plants, although poor germination prevented him from establishing the percentage of selfed *vs.* outcrossed in this taxon which requires insect aid. However, he did prove that both selfing and some crossing resulted from the insect visitations in *L. nanus latifolius*.

RATE OF FLOWER AND FRUIT DEVELOPMENT

The rate at which the flower and fruit develop and the stage at which pollination may take place differ markedly in *L. bicolor* and *L. nanus*. The flowers of the former may never open completely and pollination may accordingly take place in what is essentially the bud, to which insects are not attracted. Even though the flowers may open, pollination occurs so early in the process of anthesis and the interval available for insect intervention is so short that their effectiveness as pollinating agents is greatly reduced or eliminated even though visits should occur. Hence, *L. bicolor* is prevailingly or wholly self-pollinated, even without the aid of insects. Should outcrossing occur it must be a rare and exceptional event. *L. nanus*, on the other hand, has a considerably longer period of anthesis, and as shown above, requires the pressure provided by the insect to effect even self pollination. At the same time outcrossing is made possible, not only by the activity of insects but also by the longer time interval of receptivity.

Lupinus bicolor microphyllus was used to represent the selfing taxa and *L. nanus menkerae* the taxa requiring insect aid.

Lupinus bicolor microphyllus (Dunn 980, from a large sample collected near Ontario, California).—Measurements were started when the first flower of the first verticil was at anthesis, the banner in this case, being partially reflexed (table 1). At this time the first flower was 5 mm long, the flowers of the second verticil were 3.5 mm long, with their banners exposed and those of the third verticil were included within the calyces. When the banner was equal to or slightly exceeded the calyx it was within about 24 hours of anthesis. The flowers never completely opened in this population. During anthesis the pedicels tend to become somewhat spread but return to their erect position after fertilization. The three verticils were each about 24 to 36 hours apart in age. (The third is omitted from table 1 for simplification). In each the banners turned lavender and pollen was exuding within 24 hours after the flowers reached anthesis showing that not only had pollination occurred but

TABLE 1.—Rate of flower and fruit development of *L. bicolor microphyllus* (Dunn 980, from Ontario, California).

Date	Time	Flowers	Calyx (mm)	Flower Length (mm)	Banner	Pedicel	Pistil (mm)	Pollen	Pods (mm)	Peduncle (mm)
April	AM				1st Verticil, 5 Flowers					
8	10:00	3	....	5	half reflexed	ascending	....	....	....	27
8	10:00	2	....	5	clasping	erect	....	....	....	27
9	10:00	3	....	5	lavender	ascending	....	exuding	....	....
9	10:00	1	....	5	lavender	erect	.5 out	exuding	....	....
9	10:00	1	....	5	half reflexed	ascending	....	....	....	....
10	10:15	5	....	5	lavender	erect	.5-1.5	exuding	....	34
11	10:00	5	....	....	withering	erect	....	....	visible	34
12	10:30	5	....	....	drying	erect	....	....	5.5- 7.5	34
13	10:00	5	....	....	dry	erect	....	....	8 -10	34
14	10:00	5	....	....	....	erect	....	....	12 -14	34
					2d Verticil, 5 Flowers					Internode (mm)
8	10:00	5	3.5	3.5	whitish-green	erect	....	....	....	2
9	10:00	1	3.5	5.5	half reflexed	erect	....	....	....	4
9	10:00	4	3.5	3.5-4.5	clasping	erect	....	....	....	....
10	10:15	1	3.5	5.5	lavender	erect	....	exuding	....	5
10	10:00	2	3.5	5.5	half reflexed	ascending	....	....	....	....
10	10:00	2	3.5	5	clasping	erect	....	....	....	....
11	10:00	33	3.5	5.5	lavender	erect	out	exuding	....	7
11	10:00	2	3.5	5.5	half refl. lav.	erect	....	exuding	....	....
12	10:30	5	3.5	5.5	lavender	erect	out	....	5.5	10
13	10:00	5	3.5	....	withering	erect	....	....	5.5- 8	10
14	10:00	5	3.5	....	drying	erect	....	....	8 -11	10
15	10:00	5	3.5	....	dry	erect	....	....	10 -14	10

that the growth of the pod had already commenced. The following day in each case the style extended 0.5-1.5 mm beyond the tip of the keel. This rapid development continued, so that, within 6 days from anthesis the pods were in each case about 14 mm long, rapidly approaching full size.

Since floral measurements are some of the most reliable taxonomic criteria it is particularly interesting to note the variations in a single inflorescence. The flowers of the first verticil were mature and remained at 5 mm in length. The flowers of the second verticil matured and remained constant at 5.5 mm in length. The flowers of the third verticil, not shown, matured and remained at only 4.8 mm long. It is hard to explain this difference. It is probably due to both differences in environment from day to day and differences in the physiological constitution of the plant at the time of flowering. All of the flowers of each verticil reached and matured at the same size, probably since their maturation was at only a matter of several hours apart, at most.

Lupinus nanus menkerae (Dunn 1242, from 41 miles north of Taft, California).—The verticils were approximately 24 hours apart in age, like those of the *L. bicolor* above. There were seven verticils but only the first three are shown. The size of the flowers in this subspecies are nearly twice as large as those of the preceding subspecies of *L. bicolor*. Accompanying this increase in flower size are several other differences (table 2). The pedicels spread nearly at right angles to the rachis, whereas those of *L. bicolor* are ascending. The flowers require insect aid for pollination, as pointed out in the preceding section and evidenced here by the absence of pod set in flowers not receiving aid. That the banner must be reflexed for sometime before the stigma is receptive is indicated by the fact that the flowers generally did not set pods if pressure was applied during the first day after anthesis. That there is also some upper time limit for pollination is indicated by the fact that both flowers that had been open for 50 hours, before wing pressure was applied, failed to produce pods. The lapse in time between the reflexing of the banner and the banner color change after pollination was from 72 to 96 hours and an additional two days were required before the style had become visible. In this time interval *L. bicolor* had well developed pods.

The setting of pods on the lower verticils drew away enough of the plants energy that pod set was inhibited above (two flowers with wing pressure at 2 and 29 hours in the upper verticils failed to set pods) again probably indicating, that the growth conditions were not optimal. However, field plants have a spotty pod set and it may be that an excess of flowers is necessary to ensure some flowers the right age for pollination when the bees do visit. Plants grown in deep flats in 1947 supported more pods.

Thus it has been shown that *L. bicolor* has a very short period of flowering, that the flowers do not open at all in some cases, and that they do not require pressure to set seed. In contrast, the flowers of *L. nanus* remain open for several days and require mechanical aid to set seed. Self compatability in both cases has been shown.

THE TIME OF RECEPTIVITY OF THE STIGMA

The rates of floral development and other changes recorded above show that pollination, as indicated by the color changes of the banner, occurs in

TABLE 2.—Rate of growth of the raceme of *L. nanus menkerae* (Dunn 1242, 41 miles north of Taft, California).

Date	Time	Flowers	Flower Length (mm)	Banner	Pedicel	Wing Pressure (hours)	Flower Fall	Pods	Peduncle (mm)
April						1st Verticil, 5 Flowers			
8	10:00 AM	3	10	clasping	erect	....	....	....	....
8	10:00 AM	2	11	half reflexed	spread	....	....	....	....
8	2:30 PM	2	12	reflexed	spread	....	....	....	....
9	8:00 AM	2	12	reflexed	spread	....	....	....	58
9	9:30 AM	1	12	reflexed	spread	....	....	....	....
9	9:30 PM	1	12	reflexed	spread	12	Apr. 14	....	....
10	.... AM	2	12	reflexed	spread	24-27	....	set	60
10	.... PM	2	12	reflexed	spread	47-49	....	set	....
11-15	....	4	12	purple	erect	....	....	grew slowly	62
						2d Verticil, 5 Flowers			Internode (mm)
8	10:00 AM	5	7.5	white	erect	....	....	....	6
9	10:00 AM	5	10	blue	erect	....	....	....	12
10	8:00 AM	4	11.5	reflexed	spread	....	....	....	23
10	10:00 AM	1	11.5	reflexed	spread	....	....	....	....
11	AM	2	12	reflexed	spread	26-29	Apr. 15	....	25
11	PM	2	12	reflexed	spread	30-32	....	set	....
12	12:00 AM	1	12	reflexed	spread	50	Apr. 16	....	27
						3d Verticil, 5 Flowers			
8	10:00 AM	5	5	white	erect	....	....	....	2
9	10:00 AM	5	6.25	white	erect	....	....	....	5
10	10:00 AM	5	9.5	blue	erect	....	....	....	13
11	10:00 AM	4	11	reflexed	spread	....	....	....	25
11	10:15 AM	1	11	reflexed	spread	....	....	....	....
12	10:00 AM	5	12	reflexed	spread	....	....	....	26
13	10:00 AM	4	12	reflexed	spread	none	3:15 PM, Apr. 15	....	26
13	12:00 AM	1	12	reflexed	spread	50	Apr. 16	....	....

L. bicolor within 24 hours after anthesis; in *L. nanus menkerae* the earliest it occurs is approximately 72 hours after anthesis. There is accordingly, a considerable difference in the two species in the interval between the opening of the flower to insect visits and the time when the stigmas become receptive.

With this information as a guide, five experiments were devised to determine when the stigmas of each might be receptive. In the first experiment (using *L. bicolor*) the flowers were emasculated and pollinated by hand at various intervals after emasculation. In the second experiment (using *L. bicolor*) the stigmas were brushed clean of pollen that had not already germinated, with a camel's hair brush, and the flowers were emasculated at various intervals after the pollen had reached the stigma. In the third experiment (using *L. nanus*) wing pressure only was applied at various intervals after the banner had become reflexed. In the fourth experiment (using *L. nanus*) the flowers were emasculated and then pollinated at various intervals after the banner had become reflexed. In the fifth experiment the flowers were tagged when they opened and the time recorded as to how many hours they remained before dropping and whether any set fruit without aid. Other flowers were emasculated, the stigmas brushed clean of pollen and the time they remained on the plant recorded.

Stripping of the petals, emasculation and pollination were all performed by the use of slender tweezers. The flowers of most subspecies of *L. bicolor* and *L. micranthus* are very small, ranging from 4.6 to 7.6 mm for their mean banner length measurements and consequently require delicate handling. As a measure of safety to prevent the pollen of later flowers from falling on the stigmas, and to discourage the presence of small insects, such as thrips, minute glass capillary tubes, the outer end sealed, were slipped over the styles after emasculation and pollination. The banner was left on the flower to indicate the time when the flower would open and also to indicate any injury to the flower. In flowers injured during emasculation the banner turns lavender and becomes withered within 24 to 48 hours (the time necessary for the stigma to become receptive in *L. nanus*). In uninjured flowers the banner remains white and turgid up to 96 hours, or more, depending on the temperature. In 1946 the emasculations were all carried out prior to the time the pollen was pushed into the acumen but the loss of flowers due to early emasculation was too great to continue this procedure. Hence, in 1947 the stigmas of the flowers of the *L. bicolor* were brushed with a fine camel's-hair brush prior to opening but after the pollen had been shed and pushed partially into the acumen to remove any pollen that might have reached the stigma prior to its receptivity. Those of *L. nanus* were brushed in the same way but at anytime during the first day they were open. In both cases flower loss, due to injury, was nearly eliminated without greatly increasing the number of flowers self-pollinated.

L. BICOLOR SUBSP. AND L. MICRANTHUS

A test series was set up, pollinating at various intervals after emasculation to determine when the stigmas became receptive. An effort was made to utilize only those flowers which were just starting to shed their pollen when

they were emasculated. Even so, there was no absolute point in the time in the development of the flower from which time measurements could be made. The flowers probably varied in actual age, at the time of emasculation (± 6 hours). Only flowers emasculated after the pollen was shed or being shed had much chance for survival. Those emasculated earlier commonly develop the pedicel abscision layer and drop within 24-36 hours. This was probably due to the ease of injuring the younger flowers which had not had time for their tissues to harden somewhat, or very probably an auxin relationship, since one flower did produce a full seed set even though emasculated before its pollen was shed.

Of the three subspecies of *L. bicolor* shown in table 3 two had poor pod set when not pollinated prior to anthesis (24 hours after emasculation). Only *L. bicolor umbellatus* had a good pod set when pollinated at the time of anthesis. *L. micranthus* apparently required the earliest pollination. The one flower of the latter that remained until 48 hours after emasculation was very exceptional; most of them fell off within 24 hours, so that it was very difficult to make a test series. No further data was gathered in 1947. The small flowered colonies worked with in 1947 were emasculated and pollinated simultaneously and the larger flowered colonies were pollinated 24 hours after emasculation. Using this procedure no difficulty was encountered with intra-colonial crosses. Intra-subspecific crosses and inter-subspecific crosses will be discussed along with inter-specific crossing in the section on Cytogenetics.

The possibility that the pollen may lie on the stigma until the stigma becomes receptive has been recognized.

The length of viability of the pollen was a definite factor but cannot be completely separated or readily studied in *L. bicolor* due to the limited supply in any one flower (Refer to the pollen longevity experiments below on *L. nanus* subspecies). In one sample of *L. bicolor umbellatus* pollen was left exposed to the air for 48 hours and produced a full seed set when used in pollination.

TABLE 3.—The time of stigma receptivity in *L. bicolor* and *L. micranthus*.

Emasculation was accomplished at the time the anthers were ready or starting to shed their pollen. Anthesis is about 24 hours later. T=pods set as a result of experimental pollination. F=flowers that failed to produce pods. The percentage of the flowers that produced pods in each instance is recorded in the third column.

Hours after emasculation	L. bicolor									L. micranthus		
	microphyllus			marginatus			umbellatus					
	T	F	%	T	F	%	T	F	%	T	F	%
0	16	1	94	5	0	100	3	0	100	13	2	84
5	7	1	88	2	3	40	....	....	....	....	....	....
10	4	1	80	1	0	100	....	....	....	....	....	....
15	....	....	....	1	2	33	....	....	....	....	....	....
20	1	2	33	1	5	17	....	....	....	0	1	0
24	2	5	27	3	8	27	7	0	100	....	....	....
30-36	0	3	0	....	....	....	....	....	....	....	....	....
40	0	4	0	1	8	11	2	1	66	....	....	....
48	0	9	0	0	5	0	2	4	33	0	1	0

REMOVAL OF THE POLLEN FROM THE STIGMAS OF L. BICOLOR SUBSP. UMBELLATUS BY BRUSHING THEM AT DIFFERENT STAGES OF FLORAL DEVELOPMENT

If stigma receptivity is delayed in any of the subspecies of *L. bicolor*, it would be expected in subsp. *umbellatus*, which has the largest flowers of this species. This subspecies was accordingly chosen. The results show that its receptivity is in fact delayed.

The wings, keel, and stamens of the flowers were removed at four different stages of development and the stigmas were brushed as clean as possible with a fine camel's hair brush without actually tearing loose any pollen grains which might have germinated. The stages of floral development were 1) the banner with a tinge of lavender, taken above as an indication that fertilization had occured; 2) the banner white, the flower in full anthesis; 3) the banner just beginning to reflex; 4) the flower at approximately full length but the banner still closely clasping the wings and keel. The results are given in table 4.

The apparent discrepancy of the partially opened flowers showing a higher percentage of pod production than those that were open with white banner may be better understood when it is recalled that the banner remains open and white for only about 24 hours in addition to the small size of the sample. Observations in the greenhouse have shown that the flowers open much more rapidly in full sunlight than on cloudy days and that flowers partially open in the evening do not commonly complete opening until an hour or two after sunrise the following day. In this case about 12 hours of the 24 hour period before the flower turns lavender has already passed and the stigma will already have become receptive as is indicated by the pod production in the partially opened flowers. If the true age of each flower could be determined by some means other than color changes of the banner which are modified by other factors, then the observed discrepancy might disappear.

The data, indicate that under full light condition, the stigma becomes receptive in flowers ready for opening and is pollinated only a few hours, at most, after the banner has reflexed. Hence, if cross pollination is to be effected in the larger flowered subspecies of *L. bicolor* (which the writer has observed only one small bee visit,) any insect visits must of necessity be shortly after the flower opens. In view of this limitation and the rareness of insect visits to *L. bicolor* cross-pollination must indeed be rare.

TABLE 4.—Banner condition and pod production.

Banner condition	Produced pods	Failed	Producing pods %
Lavender	18	0	100
White, open	16	10	62
Partially open	5	1	83
Clasping other petals	0	4	0

WING PRESSURE ON L. NANUS SUBSP. AND L. VALLICOLA

Wing pressure was applied to the flowers at different intervals after the reflexing of the banner. While the wings were being pressed down, the pollen was pressed onto the stigma with the aid of small tweezers thus simulating an insect visit and insuring pollen-stigma contact. It will be remembered that in the case of *L. nanus* none of the flowers set fruit without aid.

Due to the time involved in handling each flower and the number of other experiments being conducted, the number of flowers tried at different times is rather small. However, the information shown in table 5 certainly indicates a fairly long period of stigma receptivity which begins a day or more after the flower has opened and that this time may differ in the different subspecies of *L. nanus*.

As pointed out above for *L. bicolor*, the possibility that the pollen might lie on the stigma until it became receptive, must also be considered for the subspecies of *L. nanus*. Yet in all of the subspecies of *L. nanus* tried, pollination by wing pressure less than 24 hours after the flower opened produced very poor results. *L. n. nanus* and *L. v. vallicola*, (smaller flowered) produced best results when pollinated 24 to 30 hours after opening, both here, in the pollen longevity, and in the hybridizing experiments. *L. nanus latifolius* and *L. n. menkerae*, the largest flowered subspecies, produced good pod set from 30 to 96 hours after opening and even longer.

The upper limit for the time of pollination is associated with the stimulation of the development of the pedicel abscission layer and the latter is definitely affected by heat. The flowers which turned lavender without aid in pollination had already started development of the pedicel abscission so that only those flowers in which the center of the banner was white, could be used in the wing pressure experiment.

Only a limited number of flowers remained open more than 6 days before initiating the pedicel abscission layer and this was observed to occur during

TABLE 5.—Wing pressure experiments on L. nanus and L. vallicola. T=flowers producing pods. %=percentage of flowers producing pods.

Hours after opening of wing pressure	L. nanus											
	latifolius			menkerae			nanus			L. v. vallicola		
	T	F	%	T	F	%	T	F	%	T	F	%
—24	0	4	0	....	....	....	....	....	....	....	....	....
6-12	0	4	0	0	7	0	1	12	8	0	9	0
24	6	11	35	9	13	41	7	5	58	10	10	50
30	5	3	63	5	0	100	....	....	....	....	....	....
36	2	1	67	6	1	86	....	....	....	....	....	....
42	3	0	100	2	0	100	....	....	....	....	....	....
48	24	10	71	10	6	63	13	30	30	1	1	50
56	....	....	....	7	0	100	....	....	....	....	....	....
72	18	2	90	8	6	57	5	16	24	....	....	....
96	14	7	67	4	4	50	3	5	38	....	....	....
120	5	3	63	1	5	17	0	2	0	....	....	....
144	3	5	38	....	....	....	....	....	....	....	....	....

either cloudy weather or when none of the flowers on the raceme had been pollinated. The fact that the banner color response occurred 24 hours after the 48 hour time of pollination and about 36 to 48 hours after the 24 hour time of pollination in *L. nanus latifolius* seemed to indicate that the actual time when the stigma first became receptive was probably about 36 to 48 hours after the flowers open. The total time in each case was about 72 hours after anthesis. In *L. n. nanus* and *L. v. vallicola* this color response was quicker after the 24 hour pollination time, indicating earlier stigma receptiveness.

Emasculation and pollination of flowers of L. nanus menkerae at different intervals after reflexing of the banner

This experiment was the initial experiment on the *L. nanus* group, conducted in 1946, when *L. nanus menkerae* was the only subspecies available and then in only limited numbers. The data coincided with those of the wing pressure experiment (column 2 of table 5) with the exception that all had a low percentage of flowers producing pods. In the 1946 experiments the flowers were emasculated prior to the opening of the flower and prior to the forward movement of the pollen mass. As referred to above, the flower loss was so heavy that this procedure was abandoned (4 flowers took, 19 failed, for a 19% pod development).

Time of flower drop in the absence of wing pressure; and flower drop after emasculation and brushing of the stigma without artificial pollination

The flowers were tagged on opening and the time recorded when they dropped (table 6). The advent of pedicel abscission brought about the same color change produced by pollination. This color change occurred three to five days prior to the actual falling of the flowers, which was too late to use the flowers for pollinating. The flowers shown as falling without opening, fell during a three day hot spell. More actually fell but all were not recorded. The flowers lasting the longest were produced either during cloudy weather or when the raceme had no developing pods. Here, just as in the *L. bicolor* subspecies, developing pods had an effect on the number of flowers and the time they persisted.

Out of the 1424 flowers timed in the four taxa only 32 flowers developed pods and 22 of those were in the smaller flowered *L. v. vallicola*. The remaining 10 were all of the *L. nanus latifolius* but only one produced a full pod. The partial seed set of the nine pods is probably the result of jaring of an occasional pollen grain onto the stigma in the course of tagging and emasculating. The full set may have been the result of a mistake. The large number of flowers observed that did not set pods without aid certainly leaves no doubt that this aid is essential for pollination.

The pod set in *L. v. vallicola,* however, represents a definite self pollination without aid through failure of the hair fringe to protect the stigma for some reason. Even here, the 22 pods represents only 5.9% self pollination without aid.

In the emasculated flowers that were brushed after their pollen had already

TABLE 6.—Time of flower drop in the absence of wing pressure and flower drop after emasculation and brushing without artificial pollination. N=natural, E=emasculated.

Age (hours) of flowers at time of drop	L. nanus							
	latifolius		Menkerae		nanus		L. v. vallicola	
	N	E	N	E	N	E	N	E
Unopened, 0	20	....	5	....	20	....	10	....
24	....	....	....	....	....	....	....	....
48	....	....	....	1	8	7	10	....
72	5	28	4	9	22	12	65	8
96	32	67	6	7	45	17	85	26
120	95	95	14	....	58	28	70	35
144	98	52	23	1	53	4	69	10
168	140	30	5	....	46	2	28	5
192	175	5	....	....	9	....	14	....
216	88	....	....	....	....	....	....	....
240	80	....	....	....	....	....	....	....
264	22	....	....	....	....	....	....	....
288	4	....	....	....	....	....	....	....
Totals	759	277	50	16	264	70	351	84
Produced pod								
1 Seed	3	1	....	....	....	....	....	1
2 Seed	3	....	....	....	....	....	....	....
3 Seed	3	1	....	....	....	....	2	....
full	1	....	....	....	....	....	20	....
Totals	10	2	0	0	0	0	22	1

surrounded the stigma, the flower drop was somewhat earlier in each of the four subspecies but still covered a considerable period. The notable fact is that of the 447 flowers (of the four subspecies) so treated, only three produced pods, all with incomplete seed set, two with only one seed in each. This is a .67% pod set. Hence, it is far more practical to use this method of emasculation for the pollen longevity and hybridizing experiments than to try to emasculate the flowers prior to the shedding of their pollen.

POLLEN LONGEVITY

To obtain a sufficient supply, pollen was collected from all of the flowers of one verticil, at nearly the same level and consequently nearly the same age, for each of three taxa. *L. nanus latifolius* was not only the largest flower with the largest pollen mass but this colony also produced the most flowers for experimentation. Hence, the experiment centered around *L. n. latifolius*.

The pollen was collected approximately 24 hours after it had been shed from the large anthers and before the flower opened. A portion was used immediately; the remainder was stored in a closed Petri dish and kept in the greenhouse under the same conditions to which the plants were subject. The flowers of *L. n. latifolius* were emasculated and brushed as described in the preceding section and in each case were pollinated 48 hours after the flowers opened. Those of *L. n. nanus* and *L. v. vallicola* were emasculated and

TABLE 7.—Pollen longevity. T=flowers producing pods. %=percent of flowers pollinated that produced pods.

Age of pollen (hours)	L. nanus						L. v. vallicola		
	latifolius			nanus					
	T	F	%	T	F	%	T	F	%
0	0	5	0	----	----	----	----	----	----
6	7	9	44	----	----	----	----	----	----
24	7	1	88	2	3	40	----	----	----
48	13	0	100	10	8	56	----	----	----
72	23	4	83	6	1	86	----	----	----
96	15	2	88	9	2	82	----	----	----
120	11	1	92	7	4	64	3	1	73
144	11	0	100	3	1	75	1	4	20
168	4	0	100	2(2)	4	33	1	7	13
192	----	----	----	----	----	----	1	5	17
216	----	----	----	----	----	----	----	----	----
240	----	----	----	1	11	8	----	----	----
264	3	2	60	----	----	----	0	5	0
288	----	----	----	----	----	----	----	----	----
312	4	5	44	----	----	----	----	----	----
336	----	----	----	----	----	----	----	----	----
360	4	4	50	----	----	----	----	----	----
384	----	----	----	----	----	----	----	----	----
408	0(2)	9	0	----	----	----	----	----	----

brushed in the same manner but pollinated in each case about 24 hours after they opened since the preceding experiments indicated earlier stigma receptivity. The experiments were started simultaneously but the flowers of *L. v. vallicola* were few at that time. The results are shown in table 7.

In addition to the flowers pollinated at 24 to 48 hour intervals (table 7) from these same original batches of pollen, flowers of *L. nanus latifolius* were pollinated from anthers just splitting and from others with pollen approximately 6 hours old (anthers shedding). None of the former produced pods but nearly half of the latter attempts were successful. All attempts were reasonably successful with pollen 24-36 hours old. The data indicate that the pollen must mature after shedding and that it has a long period of effectiveness. A flower of *L. n. latifolius* just opening would have pollen about 48 hours old. By the time the flower had been open 48 hours and its stigma had become receptive the pollen would accordingly be about 96 hours old and approximately in the middle of its range of viability. Failure of some flowers to set seed is probably the result of damage to their styles during manipulation, for they are delicate and easily broken.

The experiments show that the pollen remains viable from 10 to 17 days and that the range of pollen viability of each subspecies exceeds that of the period of stigma receptivity for that subspecies. The two sets of data are shown in tables 5 and 7. The extent of this overlap for *L. nanus latifolius* is illustrated in fig. 2. The maxima of pollen viability and stigma receptivity are shown to coincide. The longer period of pollen viability provides amply for selfing as long as any flowers remain on the raceme. At the same time,

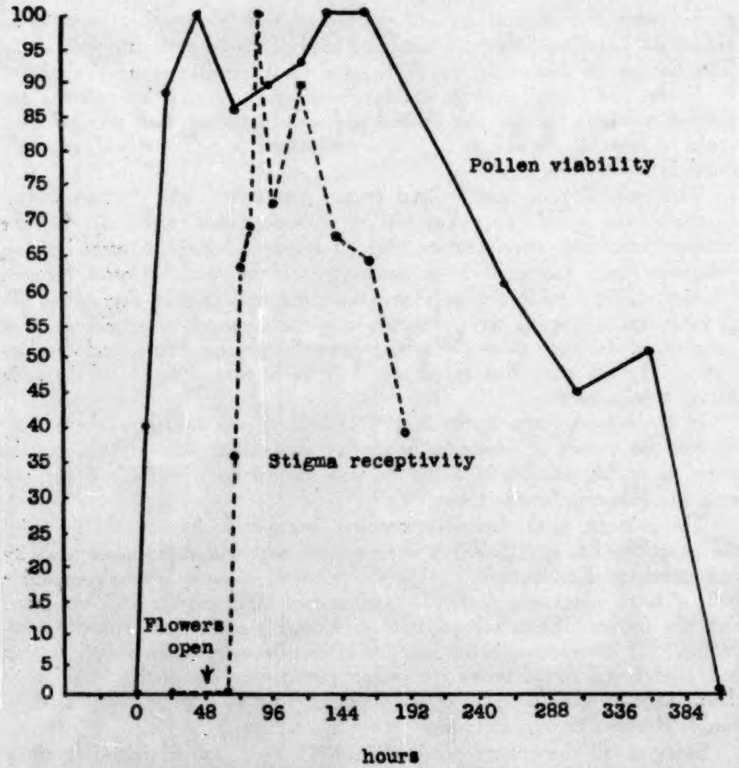

Fig. 2.—Pollen viability and stigma receptivity of *L. nanus latifolius* are expressed above as a percentage of the number of flowers producing pods. Data from tables 5 and 7 respectively. The flowers open when the pollen is about 48 hours old.

it provides for successful outcrossing to other individuals which may be at different stages of development.

The longevity of the pollen also bears a relation to insect visits, for the supply of pollen in any given acumen is not exhausted by a single visit. Even flowers visited four times in rapid succession by a bumble bee may still retain pollen. Hence, the possibility of outcrossing is increased. Nevertheless, the whole floral mechanism as well as the habits of visiting bees indicates a much greater probability of selfing. Experiments to be described in the following section point also to self compatibility and even self preference.

STUDIES IN CYTOGENETICS

Fertility—All crossfertilization attempted was at the time most favorable as indicated in the above studies. Pollination and emasculation were accom-

plished with a small tweezers and the banner was left on the flower as an indicator. Glass capillary tubes were also used as stigma caps after pollination. The number of flowers at the right stage for emasculation, particularly of *L. bicolor* and *L. micranthus*, was relatively small, so that by necessity the number available for use was limited and only a few of each type of cross could be made at any one time. However, success or failure was clearly indicated in most trials.

The possibility of intersectional crosses was tested with *L. succulentus, L. sparsiflorus* and *L. arizonicus* and all attempts failed, (table 8). In the interspecific crosses attempted in 1946 all attempts failed. Crosses between subspecies were successful in a percentage of the trials. Crosses between colonies within a subspecies were also successful to a relative degree but not as successful as crossing between members of the same colony or selfing. The members of the same colony or selfing generally yielding 100% pod development. The few cases that failed are likely to be due to injury of the style during manipulation.

In the crossing experiments in 1947 (table 9) the available flowers were all used for crosses of subspecies or species since selfing was essentially established as readily possible in all of the taxa studied both in Table 8 and the wing pressure experiments above.

The evidence again indicates complete interspecific incompatibility (with the exception of *L. v. vallicola*), a less complete inter-subspecific incompatability and intercolonial compatibility. The exception, *L. v. vallicola*, was compatible both with *L. nanus* and *L. bicolor* and crossed more readily with the latter than the former. Some subspecies of *L. bicolor* are also not markedly compatible. Of interest too, is the fact that crosses between subspecies *tridentatus* and *pipersmithii* found growing together were poorly comptaible. Although the number of trials is small, it would appear that *L. b. pipersmithii* is compatible chiefly with var. *rostratus*.

Seeds of all the crosses obtained in 1947 were planted including those in which only a single seed developed and which may be selfs. Of the F_1 planted, 27 crosses out of 68 gave 100% germination and nearly ⅔ of the crosses produced better than 60% germination.

Among the taxa in *L. bicolor* all crosses produced viable seed, matured and produced seed except those crosses with *L. b.* var. *rostratus*. These latter were either non-viable or viable up to only 25 to 30% except *L. b. pipersmithii* which crossed with 100% viability in the seed.

The taxa within *L. nanus* crossed, some producing high seed viability and others non-viable and a number that produced viable seed failed to mature and produce seeds. In one cross 92% of the seed were viable but only 10% of the plants matured. In crosses with *L. vallicola*, and *L. nanus latifolius* the

LEGEND FOR TABLES 8 & 9.—T=Seed set. The number refers to the flowers tried. F=Failure. (2)=Pods initiated but later dropped. (table 8). (*l*)=Pods initiated but later dropped and the occasional pods which produced only one seed and were hence, doubtful crosses, (table 9) These were grown and prove to be non-viable seed or were residual pollen of the female parent and hence not crosses.

TABLE 8.—Crossbreeding experiments in 1946.

		L. bicolor										L. micranthus		L. nanus	
		microphyllus			marginatus			tridentatus		umbellatus				menkerae	
Pollen from		980	1273	1414	Gorman	1265	1269a	Arvin	1289	Wms42	1002	1385	1417	1242	1247
L. b. microphyllus	980	10T		1F										3(3)F	2(*1*)F
	1273		5T												
	1414	2T		10T	3T,5F			2F	1T	3T		3F		4F	2(*1*)F
L. b. marginatus ..	Gorman			7(2)F	6T			1F	1T,5F					8(5)F	
	1265					10T									
	1269a						5T								
L. b. tridentatus ...	Arvin			1(*1*)F	1T,2F			1F		1T,1F				8(3)F	2F
	1289			2T,1F	2T,1F			1F	2T,2F					2F	5(*1*)F
L. b. umbellatus ..	Wms42			2F	1T,2F					6T				2(2)F	1F
	1002										10T				
L. micranthus	1385			3(2)F	2F					1(*1*)F			1T,2F	4F	
	1417			4(2)F	1F					5F		2T,3F	4T	2(*1*)F	3F
L. n. menkerae	1242			12F	15(3)F			1F	2F	15F		3F		35T	4T
	1247								3F	4F				3T	7T
L. sparsiflorus				7F	1F									1(*1*)F	
L. arizonicus														9(8)F	2(2)F
L. succulentus				4F										9(2)F	1F

TABLE 9.—Crossbreeding experiments in 1947.

Pollen from		L. nanus						
		latifolius		menkerae		nanus		
		2181 T / F	2456 T / F	2131 T / F	2147 T / F	2286 T / F	2297 T / F	2350 T / F
L. nanus	2181		9 0 0	7 0 6	1 2 5	6 3 15	3 4 16	5 1 10
latifolius	2456	6 1 5						
menkerae	2131	3 5 23				6 0 2	7 1 7	1 2 15
	1242	0 0 16				0 0 6	1 0 1	0 0 6
	1247	5 0 0					3 1 7	
nanus	2286	1 0 3		0 1 4				2 0 4
	2297	7 0 27				3 0 1	5 0 1	
	2350	1 0 1	0 2 3	4 0 4		12 0 6	0 2 15	
L. v. vallicola	2533	4 5 36		3 3 9		0 7 20		0 8 42
L. bicolor	965							
microphyllus	980	0 1 18						
	2204a							
	2244							0 1 7
marginatus	2245			0 2 5				
	1265							
tridentatus	2205b							
	2206b	0 0 3		0 2 4				
	2210							
pipersmithii	2205c	0 2 5					0 0 2	
var. rostratus	2211	0 0 3						
umbellatus	Wms42	0 7 20						

TABLE 9.—(continued)

Pollen from	L. v. vallicola	L. bicolor							
		microphyllus		marginatus	tridentatus			piper-smithii	var. rostratus
	2533 T / F	1414 T / F	2244 T / F	2245 T / F	2205b T / F	2206b T / F	2210 T / F	2205c T / F	2211 T / F
L. nanus	0 1 74	0 0 3	0 0 3	0 1 4		0 4 7		0 1 5	0 2 5
latifolius								0 0 4	0 1 4
menkerae	0 8 31 0 0 10	0 0 2	0 0 2	0 3 7					0 0 2
	0 14 38								
	0 2 17								
nanus	0 2 4		0 0 4	0 0 6		0 1 3		0 0 5	0 0 3
L. v. vallicola			3 0 4	3 0 2		3 1 2		0 0 2	
L. bicolor		1 0 2							
microphyllus									
				2 0 0					0 0 6
				1 0 0	1 0 0	1 0 0		0 0 3	2 0 1
marginatus	5 0 5	1 0 0	3 0 3			0 0 2		0 1 6	0 0 2
tridentatus								1 0 3 1 0 11	
pipersmithii						0 1 4			2 0 3
var. rostratus			1 0 4		2 0 0	1 1 2	2 0 0	2 0 5	
umbellatus									

one successful pod with only one seed proved non-viable. The other two subspecies of *L. nanus* did produce about 50% viable seed, while most of the crosses with the taxa of *L. bicolor* and *L. vallicola* produced viable seed.

Since the technique employed in germination normally produced nearly 100% germination in seed collected from field or selfed plants a failure in germination was considered as probably a non-viable seed.

Cytology—Somatic chromosomes in root tips, sectioned and stained with Delafields' hematoxylin (Johansen, 1940), have proved to be too numerous, crowded and too small for accurate counts to be made. Meyer's (1943) leaf smear technique did not prove any more successful. Satisfactory counts were obtained from meiotic figures using aceto-orcein or aceto-carmine as outlined by La Cour (1937 and 1947) for smears and squashes. The probable number appears to be N = 24 or 2N = 48. The collection numbers are available at UCLA as voucher sheets and duplicates will be distributed.

Subspecies or Cross	Coll. No.	N. Chromosome No.	Stage
L. nanus latifolius	Dunn 2181	24	1st microspore div.
L. n. nanus	Dunn 2350	24	1st microspore div.
L. n. menkerae X *L. v. vallicola*	Dunn 2131 X Dunn 2533	24	1st microspore div.
L. bicolor microphyllus X *microphyllus*	Dunn 980 X Dunn 1414	24	1st microspore div.
L. b. umbellatus X *microphyllus*	Wms. 42 X Dunn 1414	24	2nd meiotic div.
L. micranthus X *micranthus*	Dunn 1385 X Dunn 1417	24	1st meiotic div.
L. micranthus X *micranthus*	Dunn 1417 X Dunn 1385	24	1st meiotic div.

The reason for uncertainty of the exact number, apart from their small size (oil immersion and a 15X or 25X ocular were necessary for counting) lies in the interpretation of what is probably a longer curved chromosome, which might be two, and the haploid 25 rather than 24. Since this chromosome appears consistently and since most diploid counts reported are in even multiples of 8 or 12, the probability is that a basic N = 8 or 12 which is the same in all of the taxa examined. Furthermore, this diploid number (48) has already been reported for *L. micranthus* and *L. nanus* (Darlington and Janaki 1945). Hence, the species shown here may be actually, tetraploids or hexaploids.

The three conditions from which counts were obtained are illustrated in fig. 3. Fig. 3a is late prophase of the first meiotic division of the microspore mother cell known as "diakinesis." The chromosomes are synapsed and contracted but still scattered throughout the nuclear area. Fig. 3b is a late prophase condition of the second division of meiosis in which the chromosomes are again distinct but not yet at the equatorial plate. The clear zone in the center appears to be the first wall developing. No third and fourth cell of a tetrad could be found. Hence the conclusion that it is the second meiotic division. Fig. 3c is the late prophase of the first microspore nuclear

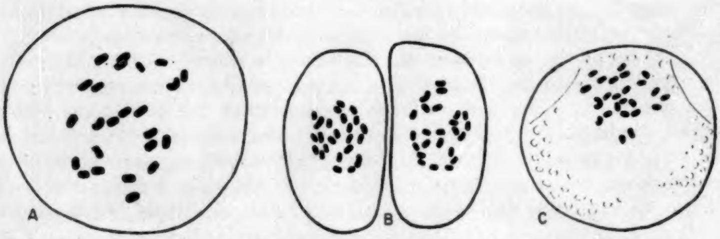

Fig. 3.—Stages from which chromosome counts were obtained.—A. Diakinesis of a cross of two colonies of *L. micranthus*, Dunn 1417 x Dunn 1385. B. Prophase of the second meiotic division in a cross between *L. bicolor umbellatus* and *L. b. microphyllus*, Wms. 42 x Dunn 1414. C. First microspore nuclear division in a cross between two colonies of *L. bicolor microphyllus*, Dunn 980 x Dunn 1414.

division as was evidenced by the development of a papillate surface of the spore, as well as, the excentric nucleus and the 3 pores for germination.

Hereditary Factors—Breeding experiments conducted to obtain information concerning the interfertility of the various entities have produced a mass of data concerning genetic factors. Most of these data have no direct bearing on the present paper and hence will be presented later. There is one character, however, that warrants consideration here, namely, failure of the flower to open. This character was found in two colonies, a pale blue *L. micranthus* (almost white, Dunn 1385), and a somewhat pale *L. bicolor microphyllus* (Dunn 980). Mass collections of both colonies were made and were found to be almost completely uniform. Two crosses and a reciprocal of the *L. micranthus* colony with the closed flowers, were made with an open blue flowered *L. micranthus* (Dunn 1417). One F_1 plant from each cross was raised in 1947 and the F_2 progeny were raised in 1948. At the same time the *L. bicolor microphyllus* with closed flowers was crossed with an open flowered *L. bicolor microphyllus* (Dunn 1414). F_1 and F_2 plants were raised.

A flower was collected from each F_2 plant, preserved in 70% alcohol and later classified. Closed or partially open flowers were only collected when all of the lower flowers that were either lavender or developing a pod were also in the same condition. Even so, the fact that the flowers tend to wither in age makes the partially open condition difficult to completely separate from those that opened and then withered (particularly in *L. micranthus*).

The *L. micranthus* cross produced 156 F_2 plants of which 28 had the banner reflexed, in 91 the banner partly reflexed and 37 remained closed producing pods without opening. The fact that there are three phenotypes, one of which is frequent enough to be near the sum of the other two, suggests a monophybrid cross bearing incomplete dominance. The Chi-square test was applied and the hypothesis found tenable.

Therefore it appears quite probable that the character of the banner clasping the other flower parts and never opening is due to a single gene, rendering the flower cleistogamous, even though the chromosome count of $2N = 48$

was suggestive of tetraploidy. Even the heterozygous, partially open flowers could not be readily visited by insects if they did visit this colony.

The frequencies observed in the *L. bicolor microphyllus* cross has nearly the expected one-fourth closed flowers but the number that reflexed was more than one-fourth. The most probable explanation of this is that the heterozygous condition which above was partially open may here be modified by the very narrow outer half of the banner. Hence no edges to be partially folded down, rendering separation of these two categories extremely difficult. Hence the suggestion that banner width may be a modifying factor.

Both *L. bicolor* and *L. micranthus* produce pods without aid so that cleistogamy has no deleterious effect. If, however, this character were present in *L. nanus* it would effectively be a lethal character since *L. nanus* has been shown to require insect aid.

SEED DISPERSAL AND GERMINATION

Lupines grow in colonies of variable size. Some colonies of both species may occupy vast areas, many acres in extent. In general, however, particularly in *L. bicolor,* these colonies are often local and cover no more than 20-40 feet in diameter. Such colonies when analyzed, are usually quite uniform in character, which suggests that they have arisen from a single individual, particularly in view of the prevalent selfing. No data are as yet available as to the increase in area of these colonies, although some are under scrutiny.

Indirect evidence upon the possibility of spread through seed dispersal is at hand. The pods of lupines split explosively along two sutures, the seeds being thrown from 15 to 20 ft. from the plant. Pods bursting in a small greenhouse can throw the seeds against the glass hard enough to be readily heard. In a field in which the main part of a colony was on one side of a road about 20 ft. wide, with curbs, a few individuals were found growing across the road indicating that the seed had spanned the 20 feet. This explosive spread of seed can readily account for the enlargement of a colony and eventually spread over the suitable available area. If one assumed a maximum spread each year of 20 ft. and that these seeds germinate and grow each year, 264 years would be required for a colony to cover an area with a radius of one mile.

New colonies probably have their origin in dispersal by seed eaters, particularly in view of the impervious seed coat. Quail, pocket mice and kangaroo rats are known to feed on the seed and the writer has observed that in colonies of lupines in an area infested with ground squirrels the immature pods have been split and the seeds removed. An indirect means of dispersal has also been suggested by Professor Loye Holmes Miller in conversation with the writer. He suggested that the known seed feeders are the common prey of hawks and owls. These birds flying with their prey, might readily scatter the seeds over a wide area directly and might also deposit the seed in the bird's feces along with the remains of the prey. Recently *L. nanus menkerae* was found in Elko Co., Nevada. It is endemic to the south end of the San Joaquin valley and has apparently been transported via livestock since the seeds could readily pass through a cow, and stockmen do use both areas alternately as winter and summer ranges.

Colonies vary in size from year to year and may disappear at intervals depending upon the weather during the period of germination. The seeds do not necessarily germinate each year but may be stored for long periods because of the hard seed coat which require either decomposition or abrasion before germination can take place.

In the experiments reported above the seed were pricked with a needle prior to planting thus permitting the entrance of both oxygen and water. Germination was best when the temperature was relatively low, near freezing at night, and the soil was moist but loose. Relatively high humidity of the air was an aid since it was then unnecessary to water the seeds after the soil was disturbed by planting. The planting depth was approximately one-half inch. Germination was prompt and abundant after abrasion and will occur during the winter season following maturation. Hence, no prolonged period of dormancy is required. That no dormancy is required was further indicated by some seed that were scattered before the pods were bagged in May 1948, forty of which germinated as a result of watering followed by a period of several cloudy days. The seed coats had had no chance to harden. Nearly all of the seed scattered, swelled but only the few grew. Still, the indication is that of a variation of the degree of seed coat hardening rather than a growth inhibition or none would have grown.

The period of natural germination is in December and January, following winter rains. Seed planted in February, March and April under essentially the same soil and moisture conditions as those planted in December and January 1947 germinated very poorly and produce very small plants. Flowering is evidently influenced by day length, for those planted late flower at about the same time as those planted in winter but were not thrifty and few set seed.

Physiological Relationship

In the course of this work various physiological reactions to growing conditions have been observed, most of which, either resulted in the death of the plants or in definite impairment of their fruiting ability. Because both modify the plant's ability to perpetuate itself in competition they are of interest at this point.

The reactions observed were concerned with such environmental relations as nutrients, water relations, heat and photoperiodism.

Lupinus nanus latifolius grew well in fertilized soils but the rest of the taxa grew better in unfertilized unsterilized soils. There was some suggestive evidence to indicate possible blockage of nutrients by others as found by Dr. Jacobson in his studies on "juvenile chlorosis" in lupines.

Excess water causing a waterlogged soil was a serious problem in some taxa causing chlorosis and death of many plants. A genetic relationship was observed. Sensitive plants could be aided by punching airholes down around the roots. Stewards and Berrys' (1934) work in tissue culture experiments would seem to supply the answer, anaerobic conditions preventing mineral absorption. The genetic susceptibility of certain taxa, however, is a factor which would be lethal in areas of high rainfall.

Summer temperatures caused death in the plants, while high temperatures

for a few days in spring were observed to cause loss of flowers at certain stages of development of many of the taxa, again, a factor in the distribution of the taxa. Went (1945) has demonstrated that heat is a critical factor in the fruit set of tomatoes. He stated that no fruit set was possible above 22°C or below 10°C for the night temperatures.

That there is also a difference in photoperiod, is suggested by the north-south limits of some subspecies and the fact that the flowering time of plants from different regions of the State is different when grown at Los Angeles. Borthwick (1947) has summarized much of the work to date on photoperiodicity, of which a great deal has centered on another legume, the soybean. Workers have found it convenient to divide the United States into nine zones of photoperiodic response, their average depth being about 150 miles.

The lupines may not be as sensitive as the soybean but the following demonstrates that there is certainly a similar effect. Colonies of F_1 and F_2 hybrids, mostly intra-specific. Crosses between colonies occuring in Los Angeles Co., flowered first. Crosses between colonies occuring in San Luis Obispo Co., flowered more than a week later, and crosses between more northerly Coast Range colonies flowered fully three weeks later. Crosses between colonies from different sections of the state flowered at intermediate times.

Although these observations are inconclusive they still indicate, the presence of physiological differences between and within the various subspecies which adapt them to their present environments. At the same time, they suggest further investigations which would demonstrate the nature of the physiological barriers which separate them. Physiological experiments on the taxa within *L. bicolor* have been conducted in the Earhart Laboratories and will be discussed in a separate paper.

RACIAL DIVERSITY AND DISTRIBUTION

L. nanus, L. vallicola and *L. bicolor* range widely throughout the western margin of the continent from British Columbia to northern Mexico. Within this area, as already implied, neither species is morphologically uniform, but is represented by a series of geographic races or subspecies. Their taxonomy has been treated in another paper, (Dunn, 1955). Using this treatment as a basis, the spatial relations of the taxa will be briefly discussed. The writer has recognized eight taxa in *L. bicolor* and three in *L. nanus* and two in *L. vallicola.* In addition, three related species shall be included, which are members of the same section, the taxa are as follows:

L. b. bicolor	*L. n. nanus*
L. b. umbellatus	*L. n. menkerae*
L. b. tridentatus	*L. n. latifolius*
L. b. pipersmithii	*L. v. vallicola*
L. b. microphyllus	*L. v. apricus*
L. b. marginatus	*L. micranthus*
L. b. var. *rostratus*	*L. affinis*
L. b. var. *trifidus*	*L. spectabilis*

Each taxon has a characteristic range and area within which it is found. The ranges of *L. bicolor, nanus, micranthus,* and *vallicola* coincide to a considerable extent, but within each species the subspecies are generally allopatric

although sometimes the margins are overlapping in area. In the event of overlapping, or in the case of *L. bicolor pipersmithii* which is included within the range of *L.b. tridentatus,* the associated entities are more or less separated ecologically. The pattern of distribution is accordingly complex.

The species cover a wide and topographically diverse area, the total range of the taxa includes an equally wide and diverse assemblage of sites, ranging from sea level to 6000 feet or more, and from the relatively mesic conditions of coastal Washington to the Colorado Desert. In general, however, the group is most abundantly represented in open valleys and on grassy slopes, and shows a preference for lighter and well drained or even sandy soils. Thus within any given area, the colonies tend to occur in the more arid situations.

The ecological range of a given entity may be wide or relatively narrow. Morphological and physiological divergence have not been parallel in all taxa. *L. micranthus,* for example, ranges from San Diego County northward to Washington and to eastern Oregon. Yet it is relatively uniform throughout this area. On the other hand, *L. bicolor,* occupying a range not dissimilar in extent, has become highly diversified. At the same time, the subspecies which comprise it are variable in extent. *L. b. tridentatus,* for example, ranges from the Tehachapi and Alamo Mts. to Oregon and from sea level to 6000 feet or more. *L.b.* var. *trifidus* on the other hand is found only along the coast in sandy soil from Santa Barbara to San Francisco. Although each entity within *L. vallicola* or *L. bicolor* has generally a characteristic range, two or more may occur together forming mixed colonies. *L.b.* var. *trifidus* and *L.b. umbellatus,* for example, are often associated. *L. vallicola apricus* is not infrequently associated with *L. v. vallicola.*

Studies of the floral mechanism reported in the preceding pages have shown that although the mechanism is basically the same in both *L. bicolor* and *L. nanus,* differences in flower size, differences in the period of receptivity all operate in such a way as to produce a different result from its operation. *L. bicolor,* if not obligatorialy selfed, is very little if at all outcrossed. *L. nanus* and other large flowered species, although probably prevailing selfed, may be and apparently is outcrossed to an undetermined degree (Burlingame, 1921). Recombination is prevented in the first, but exists in some measure in the second.

This difference in the degree of recombination is reflected in the variation pattern of the subspecies of *L. bicolor* on one hand, and *L. nanus* on the other. Colonies of the former are relatively uniform, frequently suggesting even that they may have arisen from a single individual. Colonies of the latter, however, have generally a greater range of variation, and at the same time a greater uniformity within the subspecies as a whole.

One interesting aspect of the relative distributions of *L. bicolor* and *L. nanus* lies in the fact that the former, although very largely if not wholly selfed, has apparently been more successful than the latter in diversification and adaptation to arid habitats. At first glance one might expect the contrary, inasmuch as recombination serves as a shield to mutations occurring, which although adapting an individual to a different environment, might prove fatal in the homozygous form in the environment in which it occurs.

The fact has been mentioned that *L. bicolor* var. *trifidus* and *L.b. umbel-*

latus occupy the same area in part and occur in mixed colonies. It is obvious that so far as this is true these entities must have similar ecological requirements. The persistence of differences in morphology can be accounted for by the selfing mechanism which in this case prevents recombination. Should mutations occur which condition the individual to a different environment, however, selfing and their appearance in homozygous form might eliminate them.

Although the sites in which these taxa occur appear to be similar, superficially, experience suggests that as microenvironments they may differ appreciably. Hence, it seems probable that should a given mutation appear with sufficient frequency, it might in the course of time be carried to one or another site to which it might be adapted. The possibility also exists that it might persist and multiply within its original environment and thus increase the possibility of transport to a new one. It might do this because of fluctuation in weather and the capacity of lupine seeds to remain dormant. An example of this may be seen in *L. bicolor* var. *rostratus* which is not only rare but very local, being found only in San Luis Obispo Co. near Estrella, and which like *L.b.* var. *trifidus*, exists only by virtue of its selfing mechanism. In 1946 only one plant could be found though a wide area was carefully searched. This one plant, however, was quite large and bore numerous pods. A count of the seed revealed 994 mature seed and 391 immature seed, which would have matured if the plant had not been picked. This solitary plant had 1385 seed without counting those that had already been shed. With this number of seeds as a possibility, produced by the occasional plant which may find the proper growing conditions on only an occasional year, the store of seeds of any segregating homozygous form could be similarly reproduced and increased for future transport or sufficient change in the immediate environment. (The F_1 of this plant were uniformly like the parent.) Once established in a new environment, such a varient through selfing might increase rapidly. In this way its range might readily become extended into an adjacent area, the environmental character of which is different from that in which the mutation originally appeared. If these considerations are valid, the trend toward the consequences of a sexual reproduction which obligatory selfing represents may provide a device for at least as rapid diversification and occupation of microenvironments as might be attained by outcrossing, if not more so.

CONCLUSIONS

The same floral mechanism may be conditioned in its effect in such a way as to result in obligatory self pollination in one species of a given genus and to permit outcrossing to some extent in another.

The mechanism of *Lupinus* section *micranthi* is conditioned by details of structure such as the stylar fringe of hairs, by differences in the degree to which the flower opens, by the period of receptivity of the stigma and by the duration of pollen viability.

Flower size is also a conditioning agent inasmuch as it is related to visits of the pollinating agents, chiefly or wholly bees in this case, and at the same time is correlated with the characters mentioned above.

As a result of these circumstances *L. bicolor,* the flowers of which are small relative to those of *L. nanus,* is obligatorily selfed or at most only rarely outcrossed and those of *L. nanus* are partially outcrossed.

Both species are represented by a series of geographic subspecies.

Individuals are strongly self compatible, and individuals of different colonies of the same subspecies are interfertile, although to a less degree.

Incomplete evidence indicates that the geographic subspecies of both species are less compatible and that the species are essentially incompatible. A possible slender avenue of gene exchange would exist between them, if *L. bicolor* were not strictly selfed, in *L. v. vallicola* which is compatible to some degree with certain subspecies of both species when experimentally crossed. (Morphology alone, suggests *L. v. apricus* as parallel with *L. v. vallicola*).

The occurence of both species is colonial, the colonies being of varied size, sometimes occupying many acres, but more often relatively small. Some colonies may be mixed, comprising individuals of the same species but different subspecies or of the different species, particularly in *L. bicolor*.

Migration is accomplished over short distances by explosive scattering of the seeds and over longer distances by possible transport, the principal known biological agents being birds and rodents.

The germination requirements of the seeds are rather narrowly limited. The evidence indicates that they differ with different populations. They may remain dormant in the soil for indeterminate periods. Means are accordingly at hand for accommodation to seasonal as well as regional differences of weather.

The result of these factors conditioning recombination is that the colonies of *L. bicolor* are relatively uniform, but are variable from colony to colony; those of *L. nanus* are more variable within themselves and less variable within a given region.

L. bicolor would appear to have been more successful in differentiation and adaptation to different and more stringent habitats than *L. nanus* despite the fact that it is essentially obligatorily selfed.

This fact is accounted for on the grounds that, by reason of the faculty of the seeds to remain dormant for long periods, the diversity of microenvironments within an area and the differences in weather from reproductive season to reproductive season, may permit mutations to accumulate within a given population which will be maintained and multiplied. Having accumulated, in homozygous form in the selfed population chance may carry these to other sites similar to those which find expression in their particular seasonal development. In this way the mutant populations may spread beyond their original place of origin and the species may come to occupy a range of diverse situations. Should these ecological adaptations be unaccompanied by morphological differentiation, a population will result similar to that of *L. micranthus*. Should they be accompanied by morphological differentiation a population will result similar to that of *L. bicolor.* The present subspecies of *L. bicolor, umbellatus* and var. *trifidus* may represent early steps in such a process. While *L. b. tridentatus* and var. *rostratus* may represent the very initial steps.

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The Curious Anther of Bixa—Its Structure and Dehiscence

C. S. Venkatesh
University of Delhi, Delhi, India

The family Bixaceae comprises a solitary genus *Bixa* with only one species *B. orellana* L. (Lawrence, 1951; Rendle, 1952). This plant is a native of America, and is now widely cultivated in India as an ornamental and for the dye obtained from its seeds.

Materials and Methods

Buds and open flowers, fixed in formalin-acetic-alcohol at Bangalore, were available for study. The gross features of the anthers were observed in whole mounts cleared in lactophenol. The structural details were investigated from microtome sections of material imbedded in paraffin and cut at thicknesses ranging from 8-12μ. The sections were stained with Heidenhain's iron-alum-haematoxylin followed by eosin.

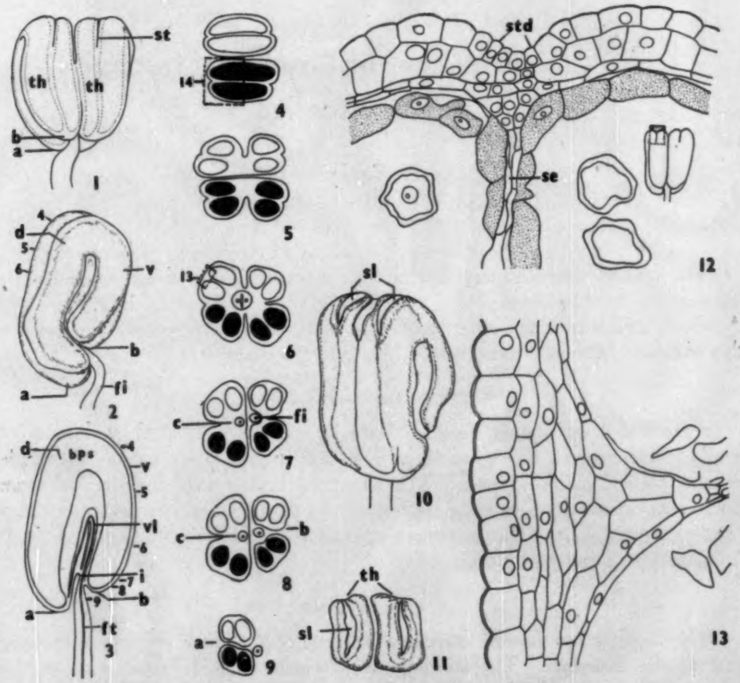
Observations

The large showy flowers contain numerous hypogynous stamens with long and slender filaments. The anthers are dithecous (figs. 1-3) but each of the two thecae is curved like a horse-shoe, whose dorsal arm (*d*) facing the periphery of the flower, is longer than the ventral (*v*) facing the centre of the flower. As a result of such curvature, the morphological base (*b*) and apex (*a*) of the anther are brought close together (fig. 2). The filament is fixed on the shorter side, which is the real base of the anther. The vascular bundle of the filament continues in the anther to form a loop (*vl*) which extends close to the apex (fig. 3).

Abbreviations

(*a*, apex of anther; *b*, its base; *bps*, bent pollen sac; *c*, connective; *d*, dorsal arm of anther; *fi*, filament; *ft*, vascular bundle of filament; *i*, point of insertion of filament with anther; *se*, septum; *sl*, slits; *st*, stomium; *std*, stomial depression; *th*, theca; *v*, ventral arm of anther; *vl*, vascular loop in the connective). (*bse*, broken septum; *fc*, fibrous cells; *l*, limit of fibrous zone; *se*, septum; *sf*, stomial fissure; *sl*, slit; *st*, stomium).

Figures 4-9 are of transections of a young anther at levels indicated in figure 3. The pollen sacs of one theca are shown in solid black. A section passing through the bend of the anther shows the two thecae free in this region and the tangentially cut pollen sacs appear laterally elongated (fig. 4). Below the bend, the thecae are still free from each other but their paired arms are adnate, so that each theca appears like a separate anther with four locules which actually correspond only to two pollen sacs (fig. 5). About the middle



Figs. 1-13.—1. Ventral view of anther (x6); 2. Side view of anther (x6); 3. Vertical plan of anther (drawn to scale); 4-9. Transections of unopened anther at levels indicated in 2, 3; pollen sacs (pollen locules) of one theca are shown in solid black (x6); 10. Dehisced anther (x6); 11. Dehisced anther viewed from above (x6); 12. V.s. part of theca of young anther in a plane indicated in accompanying diagram (x175); 13. Magnification of part of anther of same age as above in the indehiscent region indicated in 6 (x175).

of the anther the thecae as well as their arms are united in a common mass thus giving the impression of a twin anther with eight pollen locules (fig. 6). At this level, the vascular loop is cut and its two arms appear as a double vascular trace. Further down, the thecae are united by the connective but their arms are free (fig. 7). At the actual base and apex of the anther, the thecae are free from each other (figs. 8, 9).

The anther dehisces by two short slits at its tip—morphologically its middle part (figs. 10, 11).

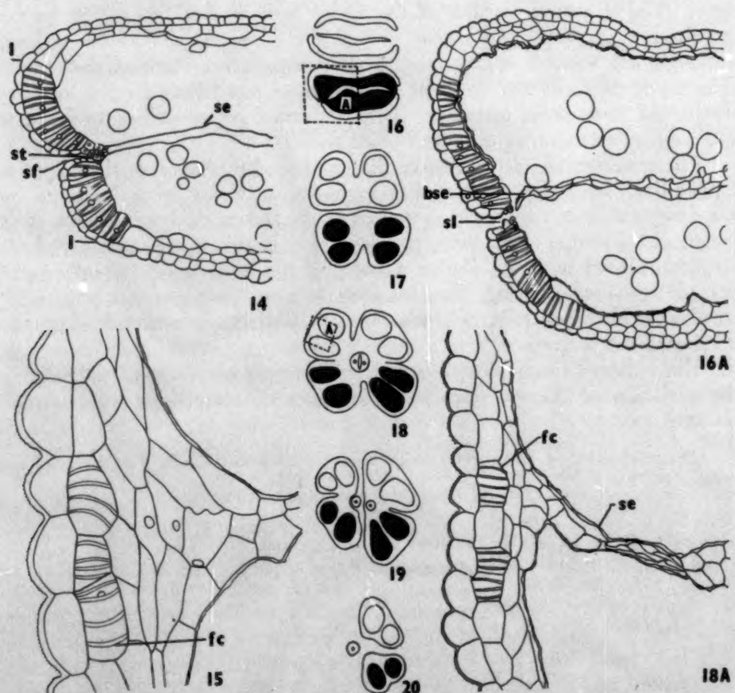
Early in development, the future lines of dehiscence are marked by two short stomial furrows around the bends of the thecae (fig. 1). Figure 12 shows a vertical section of a young anther cut through the bend of one of the thecae. Apart from a depression, the stomium proper and the wall layers of the anther are as yet undifferentiated. The furrow does not develop beyond

the region of dehiscence and the anther wall in such areas remains smooth and even (fig. 13).

Figure 14 is part of a transection through an older anther to show the structure of a stomium. The stomial furrow has deepened into a narrow fissure (*sf*) as a result of the radial enlargement of hypodermal cells flanking it. These hypodermal cells have developed characteristic secondary fibrous thickenings. Epidermal cells lying at the base of the stomial fissure are small, unthickened and overlie a group of small cells adjoining the septum.

The fibrous hypodermal layer is chiefly confined to the stomial region alone (fig. 14). It does not develop elsewhere around the sporangia. Below the limit of the short stomia, the anther wall still remains undepressed, the hypodermal cells are flat and only a few of them show fibrous thickenings (fig. 15).

The disorganization of the small-celled tissue constituting the stomia and the mechanical action of the fibrous layer cause the rupture of the mature anther wall. Such a dehiscence is strictly confined to the short length around the



Figs. 14-20.—Half of a theca at the top in t.s as indicated in 4 (x4); 15. T.s. part of old anther wall in the indehiscent region (x175); 16-20. T.s. dehisced anther at different levels (x6); 16 A, 18A. Magnifications of 16 and 18 in the parts indicated (16A.x40, 18A.x100).

curve of the anther where stomia had developed (figs. 16, 16A). The septa in this region are also broken. However, for the greater part of its length the anther remains unsplit owing to the lack of stomia and the fibrous mechanism (figs. 17-20, 18A). Even here the cells of the wall and the septa become flattened but the latter do not break so that the pollen sacs remain distinct and uncoalesced along their greater length.

SUMMARY

A unique feature of the anther of *Bixa* is the existence of curved horse shoe-like thecae. The anther is bent over itself and there has occurred a coalescence and adnation of the bent arms. The looped vascular trace affords decisive evidence of such modification. The short slit-like openings are not apical or terminal as they would appear at first sight, but they are actually situated along the morphological middle of the anther. They should therefore be described as median.

The mode of dehiscence of the anther is longitudinal, but it is of a special type. The structural features of the anther wall are such as to restrict the stomium which limits the extent of splitting. Secondly, the fibrous layer although well formed in this area, is obsolete in other parts of the anther. The few fibrous cells that do occur in the latter region fail to develop sufficient mechanical force either to rupture the unweakened anther wall or to facilitate a downward extension of the slits formed above.

The restricted slit dehiscence in *Bixa* is thus derivable from the complete longitudinal dehiscence of a typical angiospermic anther by a limitation in the development of the stomia as well as of the fibrous mechanism for a short length of the anther. Originally the dehiscence in this genus must have been longitudinal and introrse. But as a result of the bending of the anther and the restriction of splitting, the slits now face upwards and are apparently terminal. The restriction of dehiscence has thus really occurred along the middle of the anther.

The anther of *Bixa* may therefore be held to represent a transitional stage in the evolution of the true poricidal dehiscence of some other angiospermic anthers.

Acknowledgment.—I am grateful to Professor P. Maheshwari who kindly revised the manuscript.

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Pugillus Astragalorum XVIII: Miscellaneous Novelties and Reappraisals

R. C. Barneby

Wappingers Falls, New York

The following notes have grown out of general studies leading toward a revision of the North American species of *Astragalus*. Since some considerable time must elapse before I can hope to complete a useful account of this large and, in part, critical genus, I take this opportunity to publish most of the new names and combinations which I have been using in annotation of herbarium specimens, in order to make them available for use (or criticism) by other workers.

It would be impossible in a short space to give credit due to the many persons who have helped me with loans and gifts of material. I can mention here only the larger and more important collections which have been loaned to me in recent years, namely the *Astragalus* collections at: Oklahoma A. & M. College, Stillwater; Southern Methodist University, Dallas; Sul Ross College, Alpine; University of Texas, Austin; University of Washington, Seattle; and Washington State College, Pullman. I cannot hope to express in adequate terms my grateful appreciation of the courtesies extended by the curators.

Astragalus xiphoides, stat. nov.

A. convallarius var. *xiphoides* Barneby in Leafl. West. Bot. 5:30. 1947.

This species, apparently confined to the headwaters of the Little Colorado in northeast Arizona and adjacent New Mexico, is superficially similar to *A. convallarius* in growth-habit and in the strongly incurved wings and banner. As originally noted, the pod more nearly resembles that of *A. lancearius* Gray. The stipules also are those of *A. lancearius,* all being free to the base, the lower ones never united into a contrapetiolar sheath as found consistently in *A. convallarius.* This character is important nearly throughout the genus and, fortified by lesser differences, entitles *A. xiphoides* to specific rank. It might be added that the known southern limits of *A. convallarius* lie, in Utah, at the head of the Sevier in Kane County and in the Henry Mountains, Garfield County, and, in Colorado, along the upper Gunnison River.

Astragalus titanophilus, nom. et stat. nov.

A. convallarius var. *foliolatus* Barneby in Leafl. West. Bot. 5:31. 1947.

The presence of jointed leaflets in all the leaves readily distinguishes this species from *A. convallarius.* In addition the stipules are all free as in the preceding species, and I suspect a closer relationship with *A. pinonis* Jones. The latter is very similar in general aspect but may be distinguished at anthesis by the shorter pedicels (1-2 mm as opposed to 2.4-3.7 mm long) and more numerous (32-42, not 20-24) ovules, and at maturity by the broader subterete pod (5.5-8.5 mm as opposed to 3-5 mm in diameter). *A. titanophilus* is known only from an area of some 20 miles diameter about the common boundary-point of Mohave, Coconino and Yavapai counties, Arizona. The epithet *titanophilus* refers to the calcareous soils in which it is found.

Astragalus humistratus Gray var. **humivagans** (Rydb.), stat. nov.

Batidophaca humivagans Rydb. in N. Amer. Fl. 24:316. 1929.

This taxon has been treated by Clokey (Fl. Charleston Mts.:130) and by Kearney & Peebles (Arizona Flora:460) as synonymous with *A. humistratus* var. *sonorae* (Gray) Jones, but may be distinguished both morphologically and geographically as follows:

1. Pod lunately linear-oblong or narrowly oblanceolate in outline, (11) 13-20 mm long, 3.2-4 mm in diameter, (3) 4-5 times as long as wide; ovules 18-26; Arizona S of the Colorado-Gila divide, SW New Mexico and adjoining Sonora ....var. *sonorae*
1. Pod obliquely half-obovate, -ovate or plumply half-oblong in outline, 8-14 mm long, 3.5-5.7 mm in diameter, 2-3 times as long as wide; ovules 10-16; Colorado drainage of N. Arizona, SW Utah and, in scattered stations N and W to the Charleston and White Pine Mts. in Nevada ....var. *humivagans*

Some further small differences, perhaps not wholly constant, might be mentioned. The vesture of var. *sonorae* is commonly a little longer and looser, the flowers more brightly colored (reddish-purple when fresh), and the keel-petals produced into a more sharply long-attenuate porrect beak. The northern variety is nearly confined to limestone (though locally abundant on the volcanic soils of the Flagstaff Plateau), whereas var. *sonorae* seems to be consistently calcifuge. *Batidophaca stipulacea* Rydb., based on a collection from Mangas Springs, Grant Co., New Mexico (*Metcalfe* 60, NY, amplified by a topotype, *Barneby* 3040) is inseparable from var. *sonorae.*

Astragalus sesquiflorus Wats. var. **brevipes,** var. nov.

A var. *sesquifloro* pube foliolorum obtusiusculorum laxiori, calyce breviori 4 mm tantum longo, necnon pedicellis brevioribus fructiferis 1.5 (nec ad 4 mm usque) longis absimilis.

ARIZONA. Betatakin, Navajo Co., June 22, 1948, *J. T. Howell* No. 24531. Type in Herb. Calif. Acad. Sci. Navajo Mt., Coconino Co., *Milton Wetherill* No. 919/3079 (NY).

Typical *A. sesquiflorus* is apparently confined to the foot of the Zion Escarpment in southwest Utah, where it is locally plentiful on rock-ledges and in pockets of red sandstone cliffs at elevations between 5000 and 5600 feet. The leaflets are acute or mucronulate and beset (like the pod) with strictly appressed straight hairs. The calyx-tube is 2-2.8 mm and the teeth 2.2-3 mm long. At anthesis the pedicels are 2-2.5 mm becoming in fruit up to 4 mm long. The variety described here occurs at elevations of about 7000 feet and at points about 70 miles to the east on the Utah-Arizona boundary. The vesture of the pod and of the usually smaller and obtuse or obtusish leaflets is composed of sinuous or curly hairs, the flowers are a trifle smaller, with calyx-tube 1.5-2 mm and teeth 2-2.5 mm long, and the pedicels are much shorter, at anthesis about 1 mm and in fruit 1.5 mm long. Particles of red sand adhering to an isotype received from Mr. Howell suggest a habitat similar to that of var. *sesquiflorus.*

ASTRAGALUS MISER Dougl. ex Hook., sensu Cronqu. in Leafl. West. Bot. 7:17. 1953

Cronquist (l. c.) has satisfactorily demonstrated that the fragmentary type of *A. miser* (photograph, NY) is to be associated with that complex

group of forms which have passed in late years as *A. campestris* Gray (non L.) sens. lat., or as *A. decumbens* (Nutt.) Gray sens. lat. and which was broken up by Rydberg into as many as fourteen microspecies in *Homalobus*. In the same place Cronquist followed his earlier treatment (Leafl. West. Bot. 3:250-254. 1943), recognizing five varieties of *A. miser* distinguished by characters of growth-habit and, in individual cases, peculiarities of the vesture and terminal leaflet. For a number of years I have had opportunities to study the complex in the field over the greater part of its extensive range and I now feel that it is possible to carry segregation somewhat further than attempted by Cronquist, although I readily adopt his view as to the limits of the single species, a view first formulated by Marcus Jones.

From the key given below it will be seen that *A. miser* can be divided into two primary branches by the attachment of the hairs. The forms with dolabriform vesture occupy a relatively small area extending from east-central Idaho and southwestern Montana south and east to the headwaters of the Big Horn and North Platte in Wyoming. These are uniformly plants of low stature and formed a small part of Cronquist's var. *decumbens*. From the dolabriform branch it is a simple matter to detach the twig of var. *crispatus*, still known only from the Bitterroots, and clearly a minor, although in extreme form striking modification. The remainder fork into a southeastern var. *decumbens* and a northwestern var. *praeteritus*. In some individual plants which I have referred to var. *praeteritus* the suprabasal attachment of the hairs is obscure (or obscure in nearly all the hairs) and these form a gradual passage into the basifixed branch as represented by var. *tenuifolius* and var. *oblongifolius*.

The much larger division of the species, consisting of plants with basifixed hairs only, covers the same range of variation as Cronquist's vars. *miser* (formerly var. *serotinus*), *oblongifolius* (in great part) and *decumbens* combined. Our interpretations differ insofar as I distinguish two distinct forms among the taller plants of the Columbia Basin; that I recognize *Homalobus tenuifolius* Nutt. as a variety readily separable from var. *oblongifolius;* and I find good reason to separate the low-growing forms of the Rocky Mountains into a northern var. *hylophilus* and a southern var. *oblongifolius*, the last-named being thus much restricted in variability and range. Further the var. *decurrens* now seems to represent an inconsequential foliage-form of var. *oblongifolius* and is reduced to synonymy. The differential characters of each variety are discussed under the appropriate heading.

Types or isotypes have been seen of all taxa involved with the exception of *A. divergens* Blank. In this case I have followed Rydberg's reduction of his own *Homalobus camporum* to *A. divergens* as a fairly sure identification of the latter.

The synonymy is much abbreviated, since the place of publication can be readily found either in Cronquist's first paper on the group, in Rydberg's revision of *Homalobus* sect. *Campestres* (Bull. Torr. Club 50:264-268. 1923) or in N. Amer. Flora 24:268-272. 1929.

KEY TO THE VARIETIES OF A. MISER

1. Pubescence of the herbage composed wholly of basifixed hairs (2)
   2. Leaflets equally pubescent on both faces, the herbage silvery or cinereous; flowers rather large, the calyx (4.2) 4.6-6 mm, the keel (7.8) 8.6-10.7 mm long; petals

lilac or pink-purple. Pod pubescent. NE Washington and immediately adjoining British Columbia to Flathead Lake and the head of Clark's Fork in W Montana ....e. var. *miser*

2. Leaflets commonly glabrescent or quite glabrous above but, if equally pubescent on both faces then the flowers much smaller; flowers sometimes as large as the preceding but then white or whitish except for the maculate keel-tip and the pod then glabrous (3)

3. Leaflets few, (3) 7-11 to the leaf; flowers very small, the banners 6-8 mm long; pod almost exactly linear, strigulose; stems short, 1-11 cm long; ovules 8-12; SW Wyoming to NE Nevada and SE Idaho ....b. var. *tenuifolius*

3. Leaflets more numerous, 11-21 (except in an occasional early leaf); either the flowers larger or the pod oblanceolate, or the stems longer, or the ovules more numerous (or some of these combined) (4)

4. Ovary and pod consistently pubescent; ovules 13-19; Rocky Mts. of Colorado (including the Medicine Bow Range in Wyoming) and across the Colorado Basin to SW Utah and E-centr. Nevada. Plastic and often variable in the same colony as to stature and leaflet-outline ....a. var. *oblongifolius*

4. Ovary and pod either glabrous or pubescent but ovules 6-11; Rocky Mts. northward from W Wyoming and Columbia Basin (5)

5. Plants relatively tall, the stems when fully developed 1.5 dm long or more; flowers small, the keel 6-7.8 mm long; leaflets linear; Columbia Basin in Washington N to the Fraser River in British Columbia and E to the Alberta Rockies. Pod either glabrous or strigulose ....c. var. *serotinus*

5. Plants low, the stems less than 1.5 dm long; flowers nearly always larger, the keel mostly 8-10 mm long; leaflets, or most of them, of a broader type, elliptic or oval; Rocky Mts. of W Wyoming, W Montana just extending into Idaho; somewhat isolated in the Black Hills, South Dakota. Pod nearly always glabrous ....d. var. *hylophilus*

1. Pubescence of the herbage composed wholly or in great part of hairs fixed distinctly even though quite shortly above the base. Leaflets equally pubescent on either face, silvery or cinereous (6)

6. Herbage villosulous with largely twisted and loose hairs; pod minutely villosulous with short twisted hairs; Bitterroot Mts., E-centr. Idaho and adjacent Montana ....h. var. *crispatus*

6. Herbage strigulose with straight appressed or subappressed hairs; pod strigulose (7)

7. Leaflets, at least those of the leaves subtending the racemes, relatively broadly elliptic or oblanceolate; petals commonly bright pink-purple or purple-tipped, but sometimes pallid; ovules 12-18; S Montana on the Yellowstone River southward, E of the Divide, to S-centr. Wyoming ....g. var. *decumbens*

7. Leaflets narrowly linear to linear-elliptic; petals, except for the keel-tip, whitish or straw-color; ovules 7-11; SW Montana on the upper forks of the Missouri to adjacent E-centr. Idaho ....f. var. *praeteritus*

a. A. MISER var. OBLONGIFOLIUS (Rydb.) Cronqu.

Homalobus oblongifolius Rydb. *A. hylophilus* var. *oblongifolius* (Rydb.) Macbr. *A. decumbens* var. *oblongifolius* (Rydb.) Cronqu. *Homalobus humilis* Rydb. *Astragalus Carltonii* Macbr. *Homalobus microcarpus* Rydb. *H. decurrens* Rydb. *Astragalus Rydbergii* Macbr. *A. decumbens* var. *decurrens* (Rydb.) Cronqu. *A. miser* var. *decurrens* (Rydb.) Cronqu. *Homalobus Hitchcockii* Rydb.

The var. *oblongifolius* is unusually plastic, responding readily to small differences in soil, site and exposure. In the mountains of Colorado continuous colonies of plants are commonly observed on openly wooded or brushy hillsides where the reaction of the individual to shade and moisture is apparent. On dry, sunny banks or in poor stony soil the plants are dwarf and small-flowered, the leaflets are short narrow and gray-pubescent (the terminal one

either much or scarcely longer than the rest), and the pod tends to be short and narrow. But as these pass into the canopy of aspens or conifers, or into richer moister soil of a protected gully, or even to a cooler north-facing slope, the stems become imperceptibly longer, the flowers larger, the leaflets longer broader greener and thinner-textured, and the terminal leaflet tends to be much drawn out and often remote from the uppermost pair. Wherever conditions are more uniform more nearly homogeneous or nearly monomorphic populations occur. However in the heterogeneous colonies it is often possible to pick out examples of *Homalobus microcarpus, H. humilis, H. oblongifolius* and *H. decurrens* as Rydberg defined them, species evidently based on superficial and inconstant characters. It should be remarked, however, that the extreme *decurrens* form is common only on the east slope of the Front Range, and it may have some genetic basis; but even at its most distinctive, with rather tall stems and elongated linear leaflets, the terminal leaflet may be either decurrent (supposedly distinctive) or jointed to the rachis. *Homalobus Hitchcockii,* distinguished solely by the presence of black (as opposed to white) hairs on the pod, is of no taxonomic importance. The color of the hairs is inconstant in a colony of like plants and black hairs occur, if rarely and sporadically, in Colorado, Utah and Nevada.

The var. *oblongifolius* is separable from the rest of the species not upon criteria of stature, or of the size or shape of the leaflets, or of the pod's length, but by virtue of the fact that all plants known from an extensive and very natural area of dispersal are alike in their oblanceolate pubescent pods and more numerous ovules than any other form of the species with basifixed vesture.

b. **A. miser** var. **tenuifolius** (Nutt.), stat. nov.

Homalobus tenuifolius Nutt. ex T. & G., Fl. N. Amer. 1:352. 1838. *Homalobus paucijugus* Rydb. *Astragalus Garrettii* Macbr.

The present variety is distinguished from var. *oblongifolius* and var. *serotinus* by rather tenuous characters. It is less variable than either, being consistently dwarf, very slender and small-flowered, with consistently few and very narrow leaflets. In the flower, few ovules and almost exactly linear straight pod it approaches var. *serotinus* the more nearly; but that is a taller plant of widely disjunct range. In general aspect var. *decumbens* and var. *tenuifolius* are similar and have been considered synonymous; but the hair-attachment immediately sets them apart.

c. **A. miser** var. **serotinus** (Gray), comb. nov.

A. serotinus Gray, Pac. R. R. Rep. 12:51. 1860. *A. decumbens* var. *serotinus* (Gray) Jones. *Phaca serotina* (Gray) Piper. *Homalobus serotinus* (Gray) Rydb. *Astragalus campestris* var. *serotinus* (Gray) Jones. *A. Palliseri* Gray. *Homalobus Palliseri* (Gray) Rydb. *A. serotinus* var. *Palliseri* (Gray) Macbr.

Although Cronquist referred all the taller-growing plants of the Columbia Basin to one variety (*A. decumbens* var. *serotinus* or, later, *A. miser* var. *miser*), I find little difficulty in recognizing and defining two distinct races in this area. The present var. *serotinus* differs from var. *miser* in the smaller flowers, shorter calyx-teeth and green herbage, the leaflets being glabrous above. The pod may be either glabrous or minutely strigulose, but the hairs are in any case shorter and more sparsely set. The distribution of the two varieties

is mutually exclusive except perhaps along the Kettle River in southern British Columbia. The var. *serotinus* extends from the lower Wenatchee River north along the east slope of the Cascades and through the Okanogan Highland to the middle Fraser River and east to Banff and Jasper. Whereas var. *miser* represents the species along the Spokane and along the Columbia above the mouth of the Spokane, extending thence east in scattered stations to Flathead Lake and the head of Clark's Fork in northwest Montana.

The pod of var. *serotinus* is ordinarily sessile but in the Alberta Rockies it is sometimes contracted just above the base into an obscure stipelike neck up to 0.6 mm long. Plants so endowed seem in no other way different from normal var. *serotinus* of their region and I therefore dispose of *A. Palliseri*, based on an individual of this nature, as a minor variant.

In every respect var. *serotinus* seems most closely related to var. *hylophilus* from which it is distinguished mainly by greater stature. The flowers are, on the average, a little smaller, as are the pods. It is possible that the two run together in southern Alberta, but they are well separated over the rest of their ranges.

d. A. miser var. hylophilus, comb. nov.

Homalobus hylophilus Rydb. in Mem. N. Y. Bot. Gard. 1:248. 1900. *Astragalus hylophilus* (Rydb.) A. Nels. *A. campestris* var. *hylophilus* (Rydb.) Jones.

The var. *hylophilus* is usually recognizable by its broad green thin-textured leaflets alone, but these are variable in outline, sometimes all quite narrowly elliptic. Such plants occur under dry or exposed conditions or at relatively low altitudes and either in uniform populations or sporadically among broad-leaved plants, and at times closely simulate forms of var. *oblongifolius*. They differ, however, in their almost consistently glabrous pod and, without known exception, in the fewer (6-11) ovules. Toward the variety's southern limit in and near Yellowstone National Park we find an occasional individual with sparsely puberulent pod which tends to break down the distinction between the two, but such specimens are extreme examples of the broad-leaved type, and the ovule-number can be relied on. The geographic gap between vars. *hylophilus* and *oblongifolius* coincides with the low windswept saddle in the main cordillera lying between the Wind River and Medicine Bow ranges in Wyoming, the species being represented in the gap by var. *tenuifolius* and the less closely related var. *decumbens*. This barrier to migration and interbreeding has permitted the segregation of northern and southern montane races. As so often happens, the plants of the Black Hills are of the northern type.

e. A. MISER var. MISER.

A. miser Dougl. ex Hook. *Phaca misera* (Dougl.) Piper. *Tium miserum* (Dougl.) Rydb. *A. strigosus* Coult. & Fish. *A. griseopubescens* Sheld. *Homalobus strigosus* (Coult. & Fish.) Rydb. *A. serotinus* var. *strigosus* (Coult. & Fish.) Macbr.

I associate with the type, Douglas's immature fragment from the banks of the Spokane River about sixty miles above its confluence with the Columbia an approximate topotype (*Constance* 1902, WSC) which has ripe densely strigulose fruits and a few relatively large purplish flowers. These modern specimens, and others like them from Spokane County (from which no other member of the complex is known) agree with what Rydberg treated as *Homa-*

lobus strigosus, unquestionably a distinct and usually highly distinctive entity. As compared with var. *serotinus,* to which *H. strigosus* has been subordinated or reduced, it is consistently larger-flowered, more densely pubescent, and the calyx-teeth are consistently longer (1.4-2.6 as opposed to 0.7-1.3 mm long). In western Montana var. *hylophilus* might appear to occupy the range of var. *miser,* but the former occurs, nearly always, at greater altitudes, its herbage is green, its stems lower, its flowers white or whitish, and the pod is glabrous.

f. A. miser var. praeteritus, var. nov.

Pube dolabriformi totoque fere habitu var. *decumbenti* (Nutt.) Cronqu. (sens. restr.) persimilis sed allopatrica, foliolis semper omnibus anguste linearibus ovulisque minus numerosis (7-11, nec 12-18) diagnoscenda.

MONTANA. Along Ruby River, 2 miles south of Vigilante Experiment Station, Madison Co., 28 July, 1947, *C. L. Hitchcock* No. 16944. Type in Herb. Washington State College; isotype in the writer's collection. Twenty other collections seen from Madison and Beaverhead counties, Montana, and from Lemhi, Custer and northern Clark counties, Idaho; also one from Yellowstone National Park.

The present variety forms, with the two following, a major division of the species characterized by the modified attachment of the pubescence. Laying aside the minor var. *crispatus* in which the hairs of the leaves and pods have become loose and curly, we are left with an apparently rather uniform series of plants distributed along the east slope of the Rockies from the head of the North Platte to the Yellowstone and thence west across southern Montana into central Idaho, a series which can be broken up into constituent parts only by rather minute discrimination. It is remarkable, however, that the Yellowstone-Missouri divide in southern Montana coincides precisely with an abrupt alteration in ovule-number, these being uniformly 11 or less to the west and 12 or more to the southeast of this line. No other single character can be claimed as perfectly diagnostic, for the ranges of variation, while substantially different, do overlap. With few exceptions nevertheless, the southeastern plants present, even in starveling and condensed states, relatively broader leaflets, purplish and often bright purple (but occasionally ochroleucous) petals, while the racemes tend to be more compact, the hairs on the leaves a trifle longer and often more loosely ascending, and the leaflets of well developed leaves slightly more numerous. These are unsatisfactory criteria in practice, the more so as they become apparent only when individuals of equal age and vigor are compared. But there is little doubt that racial differentiation is at work, and that var. *praeteritus* merits attention.

g. A. MISER var. DECUMBENS (Nutt.) Cronqu., sens. restr.

Homalobus decumbens Nutt. ex T. & G. *Astragalus decumbens* (Nutt.) Gray. *Phaca decumbens* (Nutt.) Piper. *A. campestris* var. *decumbens* (Nutt.) Jones. *A. decumbens* var. *decumbens* (Nutt.) Cronqu. *A. divergens* Blank. *Homalobus divergens* (Blank.) Rydb. *H. camporum.* Rydb.

The relationships of this variety are discussed under the preceding. Seventeen collections have been seen indicating a range extending from Carbon, Stillwater and Sweet Grass counties, Montana, south to the Seminoe and Wind River ranges in Wyoming. Here and there in the Big Horn and Wind River mountains I have seen the interspaces on sagebrush flats and hillsides empurpled with the abundant flowers.

h. A. MISER var. CRISPATUS (Jones) Cronqu.

A. campestris var. *crispatus* Jones. *A. decumbens* var. *crispatus* (Jones) Cronqu. & Barneby.

I have seen six collections of this form, all from the slopes of the Bitterroots in Lemhi County, Idaho, and Beaverhead County, Montana. Two other gatherings from the same area illustrate a gradual passage into var. *praeteritus*.

ASTRAGALUS SPECTABILIS C. L. Porter in Rhodora 54:160. 1952

Isotypes of this species (SMU, TEX) and topotypes (*Barneby* 12710, CAS, NY) represent an exceptionally vigorous and large-flowered form of *A. detritalis* Jones, a narrow endemic of the Uinta Basin.

ASTRAGALUS VEXILLIFLEXUS Sheld.

Like many homaloboid Astragali this species is polymorphic and has given rise to geographic races sufficiently well marked to deserve systematic notice. Jones (Rev. Astrag. 97, under the later homonym, *A. pauciflorus* Hook.) has already remarked on a form with "flowers often rather cleistogamous, and then minute and white." I take this as referring to the small-flowered populations such as occur toward the southern limit of *A. vexilliflexus* on the upper Big Horn River in Wyoming. Concurrently with reduction in flower-size the stems become longer and loosely tufted or ascending and bushy-branched so that the extreme state more closely resembles *A. tenellus* Pursh than the characteristically matted *A. vexilliflexus* proper. It is suspected that *A. amphidoxus* Blank., at least as interpreted by Rydberg, represents the same or a closely similar form, but the type has not been located. For the present therefore it is preferable to go no further than point out the differential characters and to leave the question of nomenclature open. The small-flowered form, as defined in the ensuing key, has been collected mostly between 3500 and 6000 (exceptionally up to 7500) feet on barren clay bluffs, rocky knolls and shale or sandstone outcrops in the easterly foothills of the Rocky Mountains, particularly on the forks of the Big Horn, Yellowstone and upper Missouri rivers in northwest Wyoming and southwest Montana. The var. *vexilliflexus*, common in the Alberta Rockies, descends, east of the Divide, to west-central Montana, but perhaps no further than the Little Belt Mountains. Finally, isolated to the west of the Divide in the high mountains of Custer County, Idaho, there is a diminutive densely matted derivative which is described in the section following.

Astragalus vexilliflexus Sheld. var. **nubilus**, var. nov.

Prostratus intricatim ramosissimus habitu *A. Kentrophyta* var. *implexum* (Canby) Barneby simulans, sed foliolis omnibus articulatis, a var. *vexilliflexo* floribus minutis pallidis, vexillo 5.2-6.2 mm tantum longo distincta.

IDAHO. Open ridge on north of peak to east of Castle Peak, White Cloud Range, Custer Co., 8 August, 1944, *C. L. Hitchcock* & *C. V. Muhlick* No. 10857. Type in Herb. Calif. Acad. Sci.; isotypes (WSC, WTU). Railroad Ridge, Custer Co., *R. J. Davis* No. 631 (IDS, WSC).

The type of var. *nubilus* was distributed as *A. tegetarius* Wats. (a synonym of *A. Kentrophyta* var. *implexus*) and very closely resembles it in habit

of growth, being prostrate and intricately matted. As compared with var. *vexilliflexus,* the flowers are much smaller and paler, the petals being apparently whitish with purple-tipped keel. The ripe pod has yet to be collected, but when almost fully formed it is subsymmetrically lenticular and 3.5-5 mm long. The racial situation in *A. vexilliflexus* can be summarized as follows:

1. Flower relatively large, the calyx (3.3) 3.9-4.5 mm long; banner 7.2-9.3 mm long; keel 4.6-5.6 mm long; montane, E of the Continental Divide, Little Belt Mts., Montana, N to Alberta .... a. var. *vexilliflexus*
1. Flower smaller, the calyx 2.4-3.8 mm long, if more than 3.5 mm long then the banner less than 7 mm long; keel 2.9-3.5 mm long; range otherwise (2)
   2. Plants tufted, assurgent or decumbent but not densely matted; leaflets glabrescent above, at least toward the midrib; pod (5) 6-12 mm long; easterly foothills of the Rocky Mts. on the forks of the Missouri, Big Horn and Yellowstone rivers, Meagher Co., Montana S to Big Horn and Fremont counties, Wyoming; cf. discussion above.
   2. Plants densely matted, prostrate; leaflets silky-strigulose or -villosulous on both faces; subalpine in Custer Co., Idaho .... c. var. *nubilus*

Astragalus Cusickii Gray var. flexilipes, var. nov.

Caulibus plerumque elatioribus, foliolis minus numerosis superne glabris, calyce paullo breviori (tubo 3.2-4.4 mm tantum longo) necnon legumine minus inflato semi-ovoideo vel semiellipsoideo valde obliquo suturis ventrali subrecto vel adeo concava dorsali sola convexa a var. *Cusickii* aberrans.

IDAHO. Little Salmon River canyon, 3 miles north of Pollock, Idaho Co., 14 June, 1951, *Ripley* & *Barneby* No. 10709. Type in Herb. Calif. Acad. Sci.; isotypes NY, WSC. White Bird Grade, Idaho Co., *M.* & *G. Ownbey* No. 2753 (CAS, SMU, TEX, WSC). Eight other collections have been seen, all from the canyon of the Salmon River in Idaho Co.

The varieties of *A. Cusickii* may be contrasted as follows:

1. Stems 3-4 dm long; leaflets (5) 7-11 (13), commonly strigulose above, often more densely so than beneath; calyx 5-6.7 mm long; pod broadly obovoid (10) 12-22 mm in diameter when flattened in the press; Snake River Canyon and along its affluents from the west, from near Weiser downstream to the mouth of the Grande Ronde, Malheur, Union and Baker counties, Oregon, Washington and Idaho counties, Idaho, and Asotin Co., Washington .... a. var. *Cusickii*
1. Stems more slender and taller, 3.5-7 dm long; leaflets 9-15 (17), glabrous above; calyx 4-5.1 mm long; pod half-obovoid or half-ellipsoid, the ventral suture straight or a trifle concavely arched, the body 6-12 (14) mm wide when flattened; range as given in the description .... b. var. *flexilipes*

ASTRAGALUS COLLINUS Dougl. ex G. Don and A. CURVICARPUS (A. Hell.) Macbr.

The body of the pod of these two species considered collectively exhibits an almost uninterrupted sequence of variation from straight through a gentle lunate curvature, sickle-shape, an abrupt hook, and ultimately a complete ring or coil. In other respects the plants are closely similar, especially as to the tumid calyx-tube, which is gibbous-convex on the adaxial side and more or less saccate behind the insertion of the pedicel, thus somewhat resembling, as Gray remarked of his *A. cyrtoides,* the calyx of *Cuphea.* Moreover the modification in the pod's curvature is correlated with a general north-south trend in dispersal. It might almost seem that the two species, connected by the forms described as *Homalobus Laurentii* Rydb., *H. subglaber* Rydb. and *A. Whitedii*

var. *brachycodon* Barneby are no more than the extreme points in a continuous series. I find only one discontinuity, and that a small one. In *A. collinus* and *H. Laurentii* the reticulate nervature of the ripe pod is embedded in the valve-walls or sunk a trifle below the level of the intervals, which thus appear slightly elevated. In *A. curvicarpus, H. subglaber* and var. *brachycodon* the veins are elevated and enclose depressed intervals. It is convenient to regard these two groups as separate species composed in the first case of two and in the second of three varieties. Together with *A. Gibbsii* Kell., a species of limited distribution along the east base of the Sierra Nevada from Lake Tahoe to southern Lassen County, California and immediately adjoining Nevada, they form the section *Collini* sens. strict.

For a number of years I have been following Rydberg's mistaken disposition of *A. Whitedii* Piper. and *A. curvicarpus* as synonyms and employing the former epithet, which is slightly older, for *A. curvicarpus* in the sense of this article. In reality *A. Whitedii,* which is known only from a very few collections from southern Chelan County, Washington (far north of the northern limit of *A. curvicarpus*), is perfectly distinct. The calyx is neither tumid nor pouched at base, and the flowers ascend from the raceme at anthesis, unlike the retrorsely imbricated (or at least nodding) flowers of the *Collini.* It is nearly related to *A. sclerocarpus* Gray.

KEY TO A. COLLINUS, A. CURVICARPUS AND THEIR VARIETIES

1. Reticulation of the mature pod impressed; NE Oregon (but only in Wallowa, Umatilla and Morrow counties), E-centr. Idaho (Nez Perce and N Idaho counties), and N through E Washington to the head of the Okanogan and middle Fraser rivers in British Columbia (2)

2. Pod slenderly linear-oblong, 7-25 mm long, 2.5-3.4 (4) mm in diameter, straight or more rarely a little incurved, its valves vollosulous or loosely strigulose with hairs up to 0.25-0.5 mm long; ovules (10) 12-18; range as given except for Morrow Co., Oregon .... 1a. *A. collinus* var. *collinus*

2. Pod plumper and averaging shorter, obliquely ovate-oblong, gently lunate-incurved, 8-15 mm long, 3.3-4.2 mm in diameter, typically villosulous with hairs up to 0.5-1 mm long, exceptionally glabrous; ovules (7) 9-12; local in Morrow Co., Oregon .... 1b. *A. collinus* var. *Laurentii*

1. Reticulation of the pod elevated; Deschutes and John Day river-systems in transmontane Oregon, S to the Snake River Plains in SW Idaho, centr. Nevada and NE California (3)

3. Ovary and pod (at least the stipe) pubescent (if, exceptionally, glabrous, then the flowers large, the keel over 12 mm long, combined with leaflets pubescent above; Nevada and E California to SW Idaho and interior Oregon N to but not beyond the foothills of the Blue Mt. system .... 2a. *A. curvicarpus* var. *curvicarpus*

3. Ovary and pod glabrous; either the flower small, with keel mostly less than 12 mm long, or the leaflets glabrous above; NW transmontane Oregon in the drainage of the Deschutes and John Day rivers (4)

4. Flower small, the calyx 6.1-8.5 (9.3) mm long, 2.9-3.5 mm in diameter, the keel 9.4-11.6 (12.3) mm long; leaflets at least sparsely pubescent above; upper drainage of Deschutes River in Crook, Jefferson and Deschutes counties, Oregon .... 2b. *A. curvicarpus* var. *brachycodon*

4. Flower larger, the calyx more strongly inflated, (8) 9-13.6 mm long, (4) 4.5-5.8 mm in diameter, the keel 11.5-14.5 mm long; leaflets glabrous above, sparsely ciliate; lower Deschutes and John Day rivers in Wasco, Sherman, Gilliam, Wheeler and Grant counties, Oregon .... 2c. *A. curvicarpus* var. *subglaber*

1a. A. COLLINUS Dougl. var. COLLINUS

A. collinus Dougl. ex G. Don. *Phaca collina* Hook. *Homalobus collinus* (Dougl.) Rydb. *A. cyrtoides* Gray.

1b. **A. collinus var. Laurentii** (Rydb.), stat. nov.

Homalobus Laurentii Rydb. in Bull. Torr. Club 51:15. 1924. *Astragalus Laurentii* (Rydb.) Peck.

Typical var. *Laurentii* is known only from three collections (those of Lawrence cited by Rydberg and *Ripley* & *Barneby* 10783, CAS, NY, POM, US, WILLU, WSC, WTU, WYO) from "east" and "9 miles east" of Heppner which may well be derived from the same population. The plants are abundant in the station known to the writer, not more variable among themselves than usual in the genus, and differ from var. *collinus* in the remarkably small and long-villous pod. The carpological character is the sole detected difference, and could well be interpreted as marking a minor variant of *A. collinus* in which the pod varies a good deal in length and curvature. It is, in any case, an outstanding form.

About the town of Heppner and a few miles northward, near Hardman, there are found large colonies of a quite similar plant which differs both from var. *collinus* and from typical var. *Laurentii* in having a perfectly glabrous pod, lunately arcuate but a trifle longer than that of var. *Laurentii* proper. And again a short space westward we come upon the first outpost of *A. curvicarpus* var. *subglaber,* characterized by just such a pod, except that the reticulation of the valves is prominent. But var. *subglaber* is a much greener, thinly pubescent or almost glabrous plant, and the ovules are slightly more numerous. The glabrous-fruited populations in Morrow County (*Ripley* & *Barneby* 10789, 10805) are here interpreted as a minor variant of var. *Laurentii.* The uniformity of the colonies is too great to suggest recent hybridization between *A. collinus* var. *Laurentii* and *A. curvicarpus* var. *subglaber;* but some introgression between the two in past times seems most probable.

2a. A. CURVICARPUS (A. Hell.) Macbr. var. CURVICARPUS

Homalobus curvicarpus A. Hell. (based on *A. speirocarpus* var. *curvicarpus* Sheld. which was an illegitimate substitute for *A. speirocarpus* var. *falciformis* Gray; hence best considered an independent new proposition). *A. Gibbsii* var. *falciformis* (Gray) Jones. *A. Gibbsii* var. *curvicarpus* (Sheld.) Jones. *A. Whitedii* fma. *speirocarpoides* Barneby. The form with coiled pod occasional in NW Nevada and adjacent Oregon.

2b. **A. curvicarpus var. brachycodon** (Barneby), comb. nov.

A. Whitedii var. *brachycodon* Barneby in Amer. Midl. Nat. 41:496. 1949.

2c. **A. curvicarpus var. subglaber** (Rydb.), stat. nov.

Homalobus subglaber Rydb. in Bull. Torr. Club 51:17. 1924. *A. collinus* var. *subglaber* Gray ex Rydb., in syn. *A. subglaber* (Rydb.) Peck.

ASTRAGALUS REVENTUS Gray, A. CONJUNCTUS Wats. AND THEIR CLOSE ALLIES

Modern accounts of the groups of species centering around *A. reventus* and *A. conjunctus* are conflicting and very unsatisfactory. Jones (Rev. Astrag.:160) ultimately recognized only one species, subordinating *A. conjunctus* to *A. reventus* as a variety and reducing earlier segregates to synonymy;

whereas Rydberg maintained seven species disposed in two widely separated genera (N. Amer. Fl.:284-285, 393). Of the two authors Rydberg evinces by far the finer sense of discrimination, but his account is vitiated by the underlying fallacy that the presence of a septum in the pod, however narrow, carries profound phylogenetic meaning. In reality the septum may be either present or lacking in each of the following species: *A. conjunctus, A. reventus, A. riparius* (described below) and *A. hoodianus.* In Rydberg's monograph the last-named species figures in two places, as *Cnemidophacos hoodianus* when the septum is lacking and again as *Tium oxytropidoides* when it is narrowly produced, even though the supposed species described under these names are otherwise identical and confined to a very small area about the eastern mouth of the Columbia Gap. A shift of emphasis to more realistic criteria, stable and unjustly neglected differences in the flowers and stipules, results in the re-arrangement expressed by the ensuing key.

KEY TO A. REVENTUS, A. CONJUNCTUS AND THEIR NEAR RELATIVES

1. Stipules all free from each other, embracing not more than ¾ the stem's circumference (2)
  2. Pod stipitate, the stipe at least 3 mm long, equalling or far surpassing the calyx-tube (3)
    3. Banner 10-11 mm long, shorter by 2-2.5 mm than the wings. Southeast Washington and immediately adjoining Idaho .... *A. arrectus*
    3. Banner usually longer, but in any case distinctly and mostly far surpassing the wings. Here would come *A. atropubescens* Coult. & Fish., *A. remotus* (Jones) Barneby, *A. eremiticus* Sheld., sens. lat., and *A. scaphoides* Jones, irrelevant to these notes.
  2. Pod sessile or subsessile, the stipe, when present, not over 1.5 mm long, much shorter than the calyx tube (4)
    4. Stems (2) 2.5-4.5 dm long, composed of 5-10 developed internodes, the main axis evidently longer than the peduncles and raceme-axis together; ovary and 1-locular pod glabrous; ovules 14-18; SW Idaho, extending no further N than Boise Co. and S Custer Co. .... *A. adanus*
    4. Stems nearly always less than 2 dm long, composed of 2-5 (7) developed internodes, the main axis shorter than the longest inflorescences or, if taller (as sometimes in *A. Sheldoni*), then the ovary and semibilocular pod pubescent; ovules 23-36; Idaho Co., Idaho, to adjacent Oregon and Washington (5)
      5. Banner 11.5-14 mm long, 1-4 mm shorter than the wings; local along the banks of the Snake River and immediate tributaries from the mouth of the Clearwater to that of the Tucannon River, Nez Perce Co., Idaho, to Columbia Co., Washington, mostly below 1500 ft. .... *A. riparius*
      5. Banner over 15 mm long, 0.5-4 mm longer than the wings; Blue and Wallowa Mts., Oregon, and immediately adjoining parts of Washington and Idaho (6)
        6. Ovary and pod glabrous, the pod ovoid-oblong or broadly oblong-ellipsoid, 7-10 mm in diameter, very shallowly if at all sulcate dorsally, the valves not intruded or very obscurely so, the septum, if any, less than 1 mm wide; Blue Mts., Washington and Oregon .... *A. reventus*
        6. Ovary and pod pubescent, the pod narrowly oblong-ellipsoid, 4-6.3 mm in diameter, strongly grooved dorsally, the valves intruded as a definite septum 1-1.6 mm wide; Wallowa Mts., Oregon, and adjacent Idaho .... *A. Sheldoni*
1. Stipules all (or all but the uppermost) connate into a scarious contrapetiolar sheath (this sometimes ruptured in age by the expanding stem) (7)
  7. Calyx-tube cylindric or subcylindric, the tube nearly twice or a little more than twice

as long as its diameter; ovary glabrous; ovules 23-30; transmontane Oregon, mostly above 2000 ft. elevation, from Wasco to Baker Co. SE to Steens Mountain and extreme SW Idaho .... *A. conjunctus*

7. Calyx-tube campanulate, about $1\frac{1}{2}$ times as long as its diameter; ovary and pod either glabrous or pubescent; if in Oregon only along and near the Columbia River much below 2000 ft. elevation (8)

8. Ovary and sessile pod pubescent; calyx over 11 mm long; ovules 18-22; in and near the Columbia Gap of the Cascade Range, Wasco and Hood River counties, Oregon, and Klickitat Co., Washington .... *A. hoodianus*

8. Ovary glabrous or, if pubescent, then the pod stipitate and the calyx less than 1 cm long; ovules 22-32; transmontane Washington, Klickitat N to Chelan and Douglas counties (one station at the mouth of John Day River in Sherman Co., Oregon) (9)

9. Pod (glabrous) sessile; calyx-tube nearly always over 5 mm long; Klickitat, Yakima and Kittitas counties, Washington, and N Sherman Co., Oregon .... *A. reventiformis*

9. Pod (either glabrous or pubescent) stipitate, the stipe at least 3 mm long; calyx-tube 3.2-4.9 (5.8) mm long; Kittitas, Chelan and Douglas counties, Washington .... *A. Leibergi*

ASTRAGALUS REVENTUS Gray

Phaca reventa (Gray) Piper. *Cnemidophacos reventus* (Gray) Rydb.

In spite of the wide ranges attributed to this species in Jones' Revision and in Piper's Flora of Washington, *A. reventus* is in reality restricted in range to the Blue Mountains proper, where it is found in open pine-forest between three and five thousand feet elevation and extends, in scattered stations, from the head of the Birch Creek fork of the Umatilla River in Umatilla County, Oregon, northeast to the Tucannon-Grande Ronde divide in Columbia and Garfield counties, Washington. Its leading features are free stipules, large loosely spreading or nodding flowers with regularly graduated petals, and large sessile ovoid- or oblong-ellipsoid glabrous pod. The septum is either absent or obscure, not surpassing 1 mm in width. The banner varies from about 16 to 25 mm in length, and there is some indication that the species is differentiated into large-flowered southern and smaller-flowered northern populations or geographic races; but their extent and variability cannot as yet be determined. The supposed occurrence of the species in the foothills of the Cascade Range and in the Palouse country arose from misidentified specimens of *A. reventiformis* and *A. riparius* respectively. The cotypes were collected in the Blue Mountains by Douglas and by Cusick, but even at the time of publication Gray introduced an alien element in the form of a collection of *A. reventiformis* from Klickitat Valley.

Astragalus Sheldoni (Rydb.), comb. nov.

Tium Sheldoni Rydb. in N. Amer. Fl. 24:393. 1929. *A. conjunctus* var. *Sheldoni* (Rydb.) Peck.

This is close to the preceding, having essentially the same growth-habit, vesture, stipules and flowers, and differing principally in the narrower dorsally grooved pubescent pod provided with a better developed septum about 1-1.6 mm wide. Its range is limited to the northern slope of the Wallowa Mountains, along creeks flowing to the Snake River, and to closely adjacent parts of Idaho, Nez Perce and Lewis counties, Idaho. It is reported from open stony

meadows, bunch-grass prairies and rocky hillsides, mostly between 2800 and 3500 feet elevation, but perhaps a little lower in some stations.

Astragalus riparius, sp. nov.

Inter *A. reventum* Gray et *A. arrectum* Gray quasi intermedia, legumen illius sessile oblongo-ellipsoideum glabrum cum floribus hujus adscendentibus vexillo alis multo superato consocians, fortasse olim hybrida sed nunc certe species propria.

Herba perennis caulescens e radice verticali, praeter superiorem foliolorum paginam et legumen glabra undique strigulosa cinereo-viridescens; caulibus compluribus suberectis 3.5-15 (19) cm longis, pedunculis longioribus subscaposis plerumque superatis; stipulis lanceolatis vel triangularibus 3.5-7 mm longis inter se liberis; foliis (5) 10-21 cm longis, petiolis inferne subpersistentibus; foliolis 10-18-jugis anguste oblongis oblanceolatisve plerumque obtusis vel subemarginatis rarius acutiusculis (2) 4-21 mm longis in sicco mox deciduis; pedunculis validis erectis (nisi fructu ponderoso onustis declinatis) 1.4-3 dm longis striatis; racemis densiuscule (8) 12-21-floris, floribus adscendentibus, axi fructifero elongato 4-12 cm longo; pedicellis adscendentibus rectis, ad anthesin circa 1 mm, fructiferis incrassatis rigidis 2-5 mm longis, persistentibus; calycis (6.9) 7.6-10.6 mm longi nigropilosuli tubo campanulato 4.6-5.8 mm longo, (3.3) 3.6-5 mm diametro, dentibus lanceolato-subulatis (1.9) 2.2-5.2 mm longis; petalis albidis vel ochroleucis in sicco flavidis; vexillo ovato-cuneato 11.5-14.1 mm longo, 5.5-8.2 mm lato, marginibus distaliter abrupte retroflexis et facile laceratis; alis vexillo 1-3 (4) mm longioribus 12.8-17 mm longis, laminis oblanceolatis semi-ellipticis rarius lineari-oblongis obtusis 7.8-11 mm longis, (2.4) 3-4 mm latis; carina (9.4) 10.2-12.8 mm longa, laminis oblique triangularibus 4.9-6.5 mm longis, (2.6) 2.9-3.7 mm latis, abrupte per angulum subrectum in apicem obtuse deltoideum incurvis; legumine erecto sessili diu in receptaculo persistenti oblique oblongo- vel anguste ovato-ellipsoideo (1.5) 1.7-2.5 cm longo, (5.5) 6.5-10 mm diametro, recto vel paullo incurvo, basi rotundato vel truncato, distaliter in rostrum triangulari-acuminatum subcompressum abruptiuscule angustato, inferne leviter obcompresso, suturis ventrali lata dorsalique angustiori undulata bicarinato, valvulis primum carnosis viridibus demum coriaceis sublignosis brunneis stramineisve transverse ruguloso-reticulatis necnon longitudinaliter rugosis, endocarpio haud vel obscure inflexo (septo vix ad 0.6 mm usque lato), tarde per rostrum hians dehiscenti; ovulis 23-38; seminibus brunneis nigrisve laevibus sed non lucidis circa 2.6 mm longis.

WASHINGTON. Wawawai, Whitman Co., May 31, 1903, *C. V. Piper* No. 4133. Type in Herb. Washington State College. Ibid., *Piper* Nos. 3532 (WSC), 3059 (WSC), *St. John* No. 5933 (WSC). IDAHO. Hatwai Creek, Nez Perce Co., *Sandberg, MacDougal & Leiberg* No. 135 (CAS, WSC). Altogether fifteen collections have been seen, from dry bluffs and canyon-banks between 700 and 1700 feet elevation along the Snake River and tributary creeks from near the mouth of the Clearwater downstream to that of the Tucannon River, Nez Perce Co., Idaho, and Whitman and Columbia counties, Washington.

Astragalus riparius is of great theoretical interest in that it combines features of two species which, although of the same general group, would not ordinarily be thought intimately related and, furthermore, occupies a narrow strip of territory lying between the ranges of those same two species, occupying an ecological niche foreign to both. The detached pod of *A. riparius* is in form almost exactly that of *A. reventus* Gray; its flower almost precisely that of *A. arrectus* Gray, highly distinctive in the irregular graduation of the petals, the wings surpassing the shortened and modified banner. As already noted, *A. reventus* reaches its northern limit in the Blue Mountains about the head of the Tucannon, descending rarely, if ever, below the 3000 foot contour. *Astragalus arrectus* is common only in the Palouse country of Latah and Nez Perce counties, Idaho, and Lincoln County, Washington, whence it extends northwest to Grand Coulee. It is a lowland species, found on grassy hillsides, sagebrush slopes and river-bluffs, sometimes in openings of yellow pine-forest, mostly between 1300 and 2600 ft., and has been collected very close to *A.*

riparius along the Clearwater River. Its pod is entirely different from that of *A. reventus* and *riparius,* being stipitate (the stipe 2.5 -6 mm long), with narrowly ellipsoid dorsally grooved body beset with mixed black and white hairs. The striking combination of characters presented by *A. riparius* is bound to suggest hybrid origin through a chance encounter, let us suppose, of an *A. reventus* brought down from the heights to the south and temporarily established on the banks of the Snake River, with a population of *A. arrectus,* here at its southern limit. If such an encounter is easy to envisage, the subsequent course of events is open to various interpretations which I will not attempt to explore in this place, having no experimental evidence. There may be a clue here, in any case, to at least one method of speciation in *Astragalus.*

ASTRAGALUS ARRECTUS Gray

Phaca arrecta (Gray) Piper. *Tium arrectum* (Gray) Rydb.

The range and differential characters of this species are briefly discussed above. I must add that I am using the epithet *arrectus* in the sense of *A. palousensis* Piper, not having had an opportunity to reexamine the type of *A. arrectus* since disentangling the formerly confused *A. atropubescens* Coult. & Fish., which might well prove identical with the original *A. arrectus.* The type of *A. arrectus* was collected, according to Gray, "on the Kooskooskee River" (the present Clearwater), by Geyer. However Hooker had already (in London J. Bot. 6:211, under the mistaken title of *A. leucophyllus* T. & G., non Willd.) listed and partially described the same plant, giving as locality: "on layers of stiff, ferruginous clay-banks on the Trappe Mountain declivities; *upper* Kooskooskie . . ."; and stating that the fruit was *glabrous.* Using for the purposes of clarity the names *A. palousensis* and *A. atropubescens,* the types of which are both known to me, I can differentiate the two species to which the earliest name *A. arrectus* might apply as follows:

1. Petals irregularly graduated, the wings prominently surpassing the banner; flowers ascending; pod uniformly pubescent; Latah and Nez Perce counties, Idaho, NW to Grand Coulee, Washington .... *A. arrectus*
1. Petals regularly graduated, the banner surpassing the wings; flowers nodding; pod glabrous except for a very limited area in Lemhi Co., Idaho. E-centr. Idaho and SW Montana, with outlying stations in the canyons of the lower Salmon and adjacent Snake rivers in Idaho Co., Idaho .... *A. atropubescens*

ASTRAGALUS CONJUNCTUS Wats.

A. reventus var. *conjunctus* (Wats.) Jones. *Phaca conjuncta* (Wats.) Piper. *Tium conjunctum* (Wats.) Rydb.

This species is firmly and very adequately set off from all of the foregoing by its connate stipules. It is unique in its immediate group by reason of the long narrow flower and cylindric calyx-tube. Its center of dispersal lies in the John Day valley, but it extends west to the lower Deschutes River in Wasco County, Oregon, and southeast to the Malheur, to Steens Mountain, and just across into western Owyhee County, Idaho.

ASTRAGALUS HOODIANUS Howell

A. conjunctus var. *hoodianus* (Howell) Jones. *Cnemidophacos hoodianus* (Howell) Rydb. *A. conjunctus* var. *oxytropidoides* Jones. *Tium oxytropidoides* (Jones) Rydb. (err. "*oxytropoides*"). *Cnemidophacos Knowlesianus* Rydb.

This species is less variable than might be supposed from a glance at the synonymy. The first two groups of names started as independent propositions but were very quickly recognized by Jones as identical, although later resurrected and referred to distinct genera by Rydberg. *Cnemidophacos Knowlesianus* represents a common inconsequential variation with some black calyx-hairs. The species is confined to dry grassy hills and benches mostly below 500 feet elevation along the Columbia River from The Dalles downstream to Hood River, in Wasco and Hood River counties, Oregon, and on the right bank in Klickitat County, Washington. It differs from *A. conjunctus* in its broader campanulate calyx, looser or more abundant vesture, and pubescent pod of similar form but enclosing slightly fewer seeds. The calyx-teeth are nearly always longer (mostly 4.5-7.5 mm, exceptionally only 2.6 mm, as opposed to 1.3-3 mm, very rarely 4 mm long) and characteristically arched outward or distally hooked. Two collections from the hill-country south of The Dalles (near Boyd, *C. E. Hill* Nos. 18, 19, WSC) present the pubescent pod of *A. hoodianus* combined with the narrow calyx-tube and short teeth of *A. conjunctus,* strongly suggesting introgression between the two species where their otherwise mutually exclusive ranges meet or overlap.

Astragalus reventiformis (Rydb.) comb. nov.

Cnemidophacos reventiformis Rydb. in N. Amer. Fl. 24:284. 1929. *A. reventus* var. *Canbyi* Jones.

My interpretation of this species is based on study of thirty collections from Kittitas, Klickitat and Yakima counties, Washington, and one from the mouth of John Day River in Sherman County, Oregon. *Astragalus reventiformis* is closely related to *A. conjunctus,* of which it has the connate stipules (the original differential character of var. *Canbyi*) and only remotely so to *A. reventus,* with which Jones and Rydberg associated it. It is distinguished from *A. conjunctus* principally by the floral characters already brought out in the key. The pod is highly variable in size and outline. Most commonly it is broadly and plumply ovoid-acuminate with both sutures prominent at maturity, sometimes forming a winged ridge around the long diameter of the fruit, but varies by imperceptible gradations into a narrower oblong-ellipsoid form, when the dorsal suture tends to become depressed or shallowly grooved. The plump form strongly recalls the pod of *A. reventus,* the narrow form that of *A. conjunctus,* and fruiting plants of the second sort, when the flowers and circumscissile calyx have fallen, are difficult to place. We can, in any case, trace the published records of both *A. reventus* and *A. conjunctus* from the Cascade foothills in Washington to specimens of *A. reventiformis.*

ASTRAGALUS LEIBERGI Jones

A. arrectus var. *Leibergi* (Jones) Jones. *Phaca arrecta* var. *Leibergi* (Jones) Piper. *Tium Leibergi* (Jones) Rydb.

This species is very much like *A. conjunctus* in habit of growth, stipules and pod, except that the latter is elevated on a well developed stipe. The flowers are also smaller and differently proportioned. It seems remote from *A. arrectus* in stipular and floral characters and the similarity in the pod is to be attributed to parallel evolution.

The proper stems of *A. Leibergi* are normally (as in the entire group)

much shorter than the longest inflorescences, rarely surpassing 1 dm in length, and the leaflets are commonly narrow and densely cinereous or silky. In Swakane Canyon, a western affluent of the Columbia debouching about nine miles north of Wenatchee, a remarkable variant is established on steep grassy slopes among yellow pines. These plants are larger, more loosely tufted or quite strongly caulescent, and the leaves and leaflets are more ample and greener than elsewhere in the range of *A. Leibergi*. Whereas the typical form is practically confined to basaltic scablands on the plains bordering the Columbia, the Swakane Canyon plants occur on granite or serpentine gravel, sometimes associated with *Douglasia nivalis*. Although the material is plentiful (*J. W. Thompson* 8473, *C. L. Hitchcock* 17337, *Ripley* & *Barneby* 10897), I hesitate to describe, even in varietal rank, what may be no more than a vigorous ecotype.

Astragalus Minthorniae (Rydb.) Jeps. var. **gracilior** (Barneby), comb. nov.

A. ensiformis var. *gracilior* Barneby in Proc. Calif. Acad. Sci. IV, 25:158. 1944.

The present taxon was described before I had learned to distinguish between var. *Minthorniae* and var. *villosus* Barneby or to appreciate the typical phase of the species. I still feel that var. *gracilior* is related to the very rare *A. ensiformis,* which occurs about twenty-five miles to the south, but much more closely so to var. *Minthorniae,* which may be distinguished as follows:

KEY TO THE VARIETIES OF A. MINTHORNIAE

1. Stems and herbage strigulose, the hairs all strictly appressed, the longest ones about 0.7 mm long; base of the stem and lowest stipules sparingly pubescent, at least not conspicuously more densely so than the rest of the stem (2)

2. Pod narrowly or broadly oblong, straight or nearly so, 1.5-2.7 cm long, 5-6 mm in diameter; seeds 2.3-2.5 mm long; Lincoln and White Pine counties, Nevada .... var. *Minthorniae*

2. Pod linear-oblong or -oblanceolate, incurved through nearly one fourth circle, 2-3 cm long, 4-5 mm in diameter; seeds 2.7-3.4 mm long; Washington Co., Utah .... var. *gracilior*

1. Stems and herbage villous with fine spreading, sometimes curly hairs, the longest 0.8-1.5 mm long; base of the stem and lower stipules densely villous-pilose and canescent, generally more densely so than the rest; Mohave Desert, Inyo and San Bernardino counties, California, and southern Clark Co., Nevada .... var. *villosus*

ASTRAGALUS EMORYANUS (Rydb.) Cory

It is evident from the long discussion accompanying the original description of *Hamosa Emoryana* (in Bull. Torr. Club 54:327. 1927), from the specimens referred to it at the same place, and from herbarium annotations, that Rydberg really had in mind, as his new species, that form of *Astragalus Nuttallianus,* very common in western Texas, southern New Mexico and southeast Arizona in which silvery narrow and mostly acute leaflets are combined with very small flowers and glabrous fruits. However, we are bound by convention to follow his precise typification, namely Charles Wright's No. 1359 as represented in the Torrey Herbarium, and transfer the name to the related but wholly distinct species to which the specimens belong. *Astragalus Emoryanus,* as now interpreted, is distinguished from most forms of the vari-

able and polymorphic *A. Nuttallianus*, sens. lat., by its more ample flower, blunt keel tip, and retuse or emarginate leaflets combined with cinereous vesture, and from the whole species by its promptly deciduous pod. The fruit of *A. Nuttallianus* persists on the receptacle until it turns brown or black and, at least when undisturbed, dehisces while still attached to the plant; whereas that of *A. Emoryanus*, following the pattern of the related *A. Pringlei* Wats. and *A. nothoxys* Gray, is shed immediately on ripening and discharges the seeds by distal and basal dehiscence on the ground.

Astragalus Emoryanus (here including var. *terlinguensis*, discussed below) ranges the whole length of the Rio Grande valley in Texas, from El Paso to Cameron County and extends south into Nuevo León and northern Chihuahua. Somewhat disjunct stations (which may perhaps be linked by further collections to the main area) are known in Lincoln County, New Mexico, the Guadalupe Mountains in northern Culberson County, Texas, and in the east-central Texan counties of Milam and Bastrop. In the hills around El Paso, the type-locality, *A. Emoryanus* is a slender annual herb, silvery or cinereous with subappressed hairs, and similar forms occur nearly throughout the species-range. Along the lower Rio Grande the plants are sometimes much dwarfed; or sometimes, in the moist sand of washes and creek-beds, more robust and leafy than the ordinary trans-Pecos form. In southern Texas and adjoining Tamaulipas and Neuvo León the hairs of the herbage tend to become a trifle shorter and sparse, and the receptacle tends to become a little elevated as an incipient gynophore. In Nuevo León and adjacent Coahuila the wing-petals become as long or nearly as long as the banner, giving a somewhat distinctive aspect to the flower, but such plants, among which must be numbered the type of *Hamosa montereyensis* Rydb. (*Palmer* 237, GH), seem to amount to no more than a minor variant of *A. Emoryanus*.

On the south and east slopes of the Guadalupe Mountains below Signal Peak, where *A. Emoryanus* reaches its altitudinal limit of 6000 feet, the species is represented by a robust rather loosely pubescent biennial or perennial race, specimens of which were distributed by the writer as a new variety of *A. Nuttallianus* (*Ripley* & *Barneby* No. 4205) before the true nature of *A. Emoryanus* had been appreciated. In a favorable year the plants in this neighborhood may form dense mats varying from two to ten or even twelve dm in diameter, composed of up to a hundred or more primary and closely forking secondary stems, distinctly indurated at base, and already in late March covered with a mass of small but brightly colored flowers. Subsequently I have visited the locality in a dry season, when I found a few large but ailing plants growing together with their distinctively annual progeny. Perhaps a slightly more propitious microclimate provided by altitude and moisture derived from the heights above may enable some individuals to winter over.

In the Big Bend country *A. Emoryanus* is represented by the var. terlinguensis (Cory), stat. nov. (*A. terlinguensis* Cory in Rhodora 39:419. 1937), of which I have seen fourteen collections, all but two from stations scattered over Brewster County, the exceptions being from the Van Horn Mountains on the boundary of Culberson and Hudspeth counties, where the variety was collected with the typical form on the same day by B. C. Tharp (Nos. 50-260, 50-261, TEX). The variety is distinguished consistently by the short plump less strongly incurved or nearly straight pod and by the dimorphic peduncles,

the early or lower ones (sometimes all) being filiform and only 1.5-30 mm long, 1-3, rarely 4-flowered and surpassed by the subtending leaf, whereas the later ones are commonly better developed and up to 3.5-5.5 cm long. Furthermore the vesture is unusually loose by comparison with most examples of var. *Emoryanus;* and the calyx is of remarkably thin texture, becoming membranous and subdiaphanous when dried. It would appear that the short peduncles are a juvenile character, sometimes perpetuated upward along the stem-axis to maturity but as often not. And we have a few specimens from the Big Bend (such as *Cory* No. 43967, from Black Gap) in which the calyx and vesture of var. *terlinguensis* are found on the same plant with the long peduncles and slender elongate pod of var. *Emoryanus,* establishing a passage between the two.

KEY TO THE VARIETIES OF A. EMORYANUS

1. Pod linear-oblong, very gently to strongly but then evenly incurved, 1.2-2 (2.2) cm long, (2) 2.2-3.3 mm in diameter, 5-6.5 times as long as wide; peduncles homomorphic, equalling or surpassing the leaves; vesture mostly appressed or subappressed, the hairs in any case distinctly shorter than in the next where the two coincide in range .... var. *Emoryanus*
1. Pod more broadly and plumply lance-oblong, nearly straight or very slightly incurved, 0.8-1.4 cm long, (2.5) 3-3.7 mm in diameter, 3-4.3 times as long as wide; peduncles mostly dimorphic, the lower ones (sometimes all) filiform and 1.5-30 mm long, surpassed by the leaves. vesture composed of rather stiff straight and spreading or incurved-ascending hairs up to (0.5) 0.6-0.75 mm long. SE Hudspeth and Brewster counties, Texas .... var. *terlinguensis*

ASTRAGALUS CRASSICARPUS Nutt. AND RELATED SPECIES

The group of species with which we are here concerned is equivalent to the section *Sarcocarpi* of Gray and Jones or the genus *Geoprumnon* Rydb. Although we find among them some of the commonest and most widespread Astragali of the prairies, plains and east slope of the Rocky Mountains, we still lack a realistic account of them, that of Rydberg (in Bull. Torr. Club 53:161-165, repeated in N. Amer. Fl. 24:460-462) being especially open to criticism. I follow a long tradition when I include in the key the very distinctive *A. tennesseensis* Gray which, on account of its modified pod, may well form the type of a section apart. My views are summarized in the following:

KEY TO A. CRASSICARPUS, ITS VARIETIES, AND RELATED SPECIES

1. Plants hirsute with fine straight spreading hairs up to 2-3.5 mm long, the stems densely so and shaggy; valves of the thinly hirsute pod becoming coarsely alveolate-reticulate in ripening, the exocarp and mesocarp ultimately decaying (by over-winter weathering on the ground) and revealing the leathery endocarp enclosed in a loose reticulum of fibres; N and centr. Illinois; centr. Tennessee; ? and N Alabama .... *A. tennesseensis*
1. Plants variably pubescent, but the longest hairs very rarely over 1.5 mm long, the stems in any case not shaggy-hirsute; valves of the glabrous or shortly pilosulous pod variously roughened or wrinkled when ripe, both exocarp and endocarp long enduring and separated by a thick mesocarpic layer of large cells, these at first filled with watery juice, at length forming a light and fragile pith; widespread (2)
   2. Ovary and pod (except exceptionally in W Texas) glabrous, the walls of the ripe pod 2-5 mm thick (except rarely in E-centr. Arizona and centr. New Mexico): calyx early becoming scarious fragile and circumscissile above the disc; stems (except of *A. crassicarpus* var. *Berlandieri,* local in S-centr. Texas) arising together from the crown of the taproot or from the short divisions of a knotty

root-crown at or just below the level of the soil; ovules (38) 45-77; widespread, but not extending S in Texas to the Balcones Escarpment (2)

3. Pod broadly oblong-ellipsoid or subglobose, 7/8 as long to 1½ times as long as its greatest diameter; stipules glabrous dorsally; leaflets commonly glabrous or at least glabrescent along the midvein on the upper face; widespread (4)

4. Calyx, like the pedicels, densely villosulous-tomentulose (at least proximally, commonly throughout) with short entangled and some longer ascending cream-colored or brownish hairs; petals greenish-white or cream-colored, sometimes suffused with pink or lilac; racemes 13-25-flowered; peduncles 6-16 cm long; plants robust, the stems commonly coarse and fistular, ascending, (2.5) 3.5-6 dm long; pod large, 2.5-3.2 cm long; Illinois to Louisiana and E Texas ....1d. *A. crassicarpus* var. *trichocalyx*

4. Calyx strigulose, pilosulous or ascending-pilose with mixed black and white or largely black hairs; petals purple, lilac, flesh-colored or pure white; peduncles shorter, (0.8) 2-6.5 (10) cm long; plants commonly less robust, the stems decumbent with ascending tips, 1-4 (5) dm long; widespread over the plains and prairies but, where entering or approaching the range of the last, the racemes composed of 15 or less flowers and the petals (disregarding rare albino forms) bright purple (5)

5. Stems arising together from the crown of the taproot at or just below soil-level; if purple-flowered and of E Texas then the ovules 52-68 (6)

6. Petals all purple or lilac; herbage bright green (at least below the vesture); mostly E of longitude 120° and below 4000 feet elevation ....1a. *A. crassicarpus* var. *crassicarpus*

6. Petals white (except for the faintly maculate keel-tip) but sometimes suffused with pale pink or flesh-color; herbage pallid- or yellowish-green; mostly W of longitude 120° and above 3500 feet elevation ....1b. *A. crassicarpus* var. *Paysoni*

5. Stems arising singly or few together from slender widely forking subterranean caudex-branches; ovules 34-50; local in SE Texas ....1c. *A. crassicarpus* var. *Berlandieri*

3. Pod narrowly oblong, 3-4 times longer than wide; stipules strigulose dorsally; leaflets equally cinereous-strigulose on both faces; local in S Eddy Co., New Mexico, and immediately adjoining Texas ....2. *A. gypsodes*

2. Ovary and pod pubescent, the walls of the ripe pod less than 2 mm thick; calyx becoming papery-scarious, ruptured but persistent about the base of the pod; stems arising singly and few together from buds on widely branching subterranean rhizome-like caudex-branches ....3. *A. plattensis*

1a. A. CRASSICARPUS Nutt. var. CRASSICARPUS

Geoprumnon crassicarpum (Nutt.) Rydb. *A. caryocarpus* Ker. *Phaca caryocarpa* (Ker) MacMill. *A. carnosus* Pursh, in part, emend Nutt. (Gen. 2:100).

Some botanists, among them Gray and, later, Fernald (in Gray's Man., Ed. 8), have discarded the name *A. crassicarpus* in favor of the slightly later *A. caryocarpus*. Their reasons appear to be three: that *A. crassicarpus* was too briefly described to be surely recognizable; that there is doubt as to the authorship of the Fraser Brothers' Catalogue; or that the Catalogue itself cannot be accepted as a valid medium of publication. To these arguments I would reply that there is no other *Astragalus* "above the River Platte" which has the fruit "about the size and form of *A. physodes*, but thick and succulent," and that Nuttall used nearly the same phrase in his discussion (Gen. 2:100) of *A. carnosus*, of which the identity is certain; that Nuttall, in the work just cited, acknowledged his responsibility for the names in the Catalogue (cf. *Amorpha canescens*); and that the validity of the whole catalogue is outside the jurisdic-

tion of any one author, but should be decided by a competent international committee. The three names *A. carnosus, A. caryocarpus* and *A. crassicarpus* were all based on material, or on cultivated progeny of material collected by Nuttall and Bradbury together on the exploration of the Platte River, and their identity can hardly be questioned.

The var. *crassicarpus* is dispersed nearly throughout the Mississippi and lower Missouri basins from western Arkansas to Minnesota, north into Manitoba, west to northeast and trans-Pecos Texas, eastern Colorado, central Nebraska and the Dakotas. In all probability it was formerly much commoner on the prairies than at present, being now found principally along protected rights of way. To the south it is still frequent on rocky hillsides and about the edge of oak-thickets and is capable of establishing itself in abandoned pastures or other fallow land. Its range lies mostly below the 4000 foot contour, but it ascends to 4500 and even 5800 feet elevation in Texas and at least to 4450 feet elevation in Colorado, there passing imperceptibly into the poorly differentiated var. *Paysoni.*

In western Texas var. *crassicarpus* has thrown out some remarkable forms. On the limestone prairies of Irion Co., and again in the Glass Mountains of Brewster Co., densely pubescent plants occur in which ovary and even mature pod are strigulose. They seem to differ in no other way from the ordinary prairie form. On Ord Mountain in Brewster County a local race combines puberulent pod with exceptionally large flowers and long calyx-teeth. But glabrous-fruited and apparently quite normal var. *crassicarpus* is also found in the same general region, the plants differing however from the prairie type (as also from the sympatric races with pubescent pod) in the small number (38-44) of ovules. These interesting forms require further study.

1b. **A. crassicarpus** var. **Paysoni** (Kelso), comb. nov.

A. succulentus var. *Paysoni* Kelso in Rhodora 39:151. 1937. ? *A. succulentus* Richards. *Geoprumnon succulentum* (Richards.) Rydb. *A. prunifer* Rydb.

The var. *Paysoni* was originally separated from the montane form of *A. crassicarpus* long passing as *A. succulentus* on pubescence-characters of minimal importance, but we are obliged to take up the name in the rank of variety. The type was collected on Big Creek near Encampment, Carbon County, Wyoming (*Payson* & *Payson* 2514, US) and that of *A. prunifer* close by, at Medicine Bow. Both represent the race of *A. crassicarpus* native to the east slope of the Rocky Mountains from southern Alberta to southern Colorado and extending feebly across the continental divide to the head of Deer Lodge Valley in southwest Montana. I can find no consistent criterion other than the feeble differences in color brought out in the key to discriminate between var. *crassicarpus* and var. *Paysoni.* For the most part, however, the herbage of the latter is more sparsely beset with shorter hairs, the inflorescence is either more thinly pilosulous or merely strigulose, and the flowers are, on the average, distinctly larger. The ovules of var. *crassicarpus* (with some few exceptions mentioned above) number 52 to 68, those of var. *Paysoni* (40) 47 to 59, averaging 60 and 52 (in 60 counts of the former, 43 counts of the latter). The shape of the leaflets is not in reality strongly correlated with flower-color, as assumed by Rydberg, though they are perhaps, on the average, a little wider in var. *Paysoni.*

Along the higher prairies at the foot of the Rocky Mountains we find many forms intermediate between the two varieties, and specimens from this area are difficult to assign to a particular category, especially when in fruit. I have seen, for example, one such plant from as far south and east as the Black Mesa in Cimarron County, Oklahoma, which may mark the limit of dispersal in this direction. Typical var. *Paysoni* is not known to me from south of Huerfano County, Colorado, but a related form carries the species on, in scattered stations, to south-central New Mexico and eastern Arizona. This southern form resembles var. *Paysoni* in nearly every way, but the pod is strongly inflated, with thin walls and a large empty cavity, very unlike the solid fruit of *A. crassicarpus* as a whole. The material at hand is as yet insufficient for adequate analysis, but a distinct taxon is assuredly involved. This form has been collected in southern Apache County, Arizona (between Eagar and Nutrioso, *Ripley* & *Barneby* 5089, 8430) and in the Sacramento Mountains of Otero County, New Mexico (near Mayhill, *Barneby* 11158), and it is likely that the *A. crassicarpus* cited from Horse Spring in Socorro County, New Mexico, by Wooton and Standley in their State flora will provide, when critically examined, an intermediate station.

I cannot endorse Rydberg's assumption that A. *succulentus* Richards. represents the same form as *A. prunifer* Rydb. without recourse to the type of the former. It is true that Richardson described the flower as pale, but his plant came from "sandy plains in the neighbourhood of Carlton," that is, from the North Fork of the Saskatchewan above the present Prince Albert. The material that I have seen from this area, admittedly meagre, appears to belong rather to var. *crassicarpus* than to var. *Paysoni,* as might be expected from their known ranges southward. I therefore list *A. succulentus* as a doubtful synonym. Providing that it belongs to the species *A. crassicarpus* sens. lat., as seems virtually certain, and that the arrangement proposed here is accepted, its identity from the nomenclatural point of view is academic.

1c. A. crassicarpus var. Berlandieri, nom. nov.

A. mexicanus A. DC. in Mem. Soc. Bot. Genève 6:224. 1833.

This variety is ultimately distinguished from var. *crassicarpus* by the peculiar subterranean caudex-branches and resultantly different growth-habit, first noticed by Jones (Contrib. West. Bot. 17:28), a character shared by *A. plattensis* but foreign to the rest of its species. If we could associate the growth-form with any one other character assigned by Rydberg to *G. mexicanum,* we might accept it as a separate species, but this is hardly the case. The very large pod and flower (though neither "3 cm. long" nor "white or ochroleucous", for the purple banner varies from 18 to 25, exceptionally 27 mm in length) are not characteristic of such plants. In the region of Austin, especially, the flowers and pods are highly variable in size, and at the low extreme fall well within the range of variability of normal var. *crassicarpus.* It is rather remarkable that even the largest flowers and pods of var. *Berlandieri* should produce invariably fewer ovules, and a study of the seeds might produce interesting results. Really ripe fruit is seldom collected, owing to the long period required for ripening, and a valid comparison of the seeds has not been feasible.

The var. *Berlandieri* is found on brushy hillsides, gravelly flats among oak-

thickets, in loamy or silty soils overlying limestone rocks at elevations below 1500 feet. It is locally plentiful on and near the southeast escarpment of Edwards Plateau and extends rarely a short distance out onto the coastal plain, Kerr, Gillespie, Washington and Victoria counties marking the limits of its known range. The type, known to me only from DeCandolle's figure, is a plant raised at Geneva from seeds collected by Berlandier on the banks of the Guadelupe River. They must have come from the heart of the range of the taxon under consideration, and from far south of the southern limit of var. *trichocalyx*, to which the epithet *mexicanus* was erroneously transferred by Gray.

In reducing *A. mexicanus* to varietal rank I have exercised the privilege of supplying a new epithet, the adjective *mexicanus* being absurd when applied to this local Texan endemic.

1d. A. CRASSICARPUS var. TRICHOCALYX (Nutt.) Barneby ap. Gleason

A. trichocalyx Nutt. *Geoprumnon trichocalyx* (Nutt.) Rydb. *A. mexicanus* var. *trichocalyx* (Nutt.) Fern.

This well known variety is most common in and nearly confined to the Ozarkian highland in Oklahoma, Missouri, Illinois and Arkansas, thence extending south only to northeast Texas and adjoining Louisiana. I agree fully with Gray, who said of it (in Proc. Amer. Acad. 6:193): "Some of the Texan forms especially, with less hairy calyx, run much too close to the foregoing [*A. caryocarpus*]; but, on the whole, this pale-flowered and coarser fleshy-fruited *Astragalus* seems to hold distinct"; it will perhaps remain a matter of individual preference or individual stress on the relative importance of likenesses and differences, whether it receives the rank of species or variety.

2. **Astragalus gypsodes**, sp. nov.

A. crassicarpo Nutt. affinis sed legumine cylindrico nec suborbiculari, stipulis dorso strigulosis, foliolisque utrinque cinereo-strigulosis facile separanda. Habitat etiam in solo gypsaceo ubi *A. crassicarpus* hucusque nunquam obvia.

Herba perennis humilis sed robusta, praeter petalos et legumina glaberrima pilis rectis basifixis appressis undique striguloso-cinerea; caulibus compluribus e radicis verticalis validae collo pluricipiti adscendentibus (0.5) 1-3 (3.5) dm longis simplicibus; stipulis deltoideis vel deltoideo-acuminatis submembranaceis 2-7 (9) mm longis semiamplexicaulibus inter se liberis; foliis (4) 6-18 cm longis; foliolis 7-12 (14)-jugis ellipticis vel anguste ovato-lanceolatis acutiusculis obtusisve rarius oblongo-obovatis retusis 5-20 mm longis; pedunculis 3.5-10 cm longis, ad anthesin erectis, fructu ponderoso onustis demum declinatis; racemis laxiuscule (10) 15-30-floris, axi fructifero 3.5-11.5 cm longo; bracteis 2.5-6 mm longis; pedicellis floriferis 1.3-2.3 mm longis, frutiferis incrassatis 2 3.4 mm longis persistentibus; calycis fere semper bracteolati purpurascentis albo- vel nigro-strigulosi 10.4-14.7 mm longi tubo cylindro-campanulato 7.3-10 mm longo, 3.8-5 mm diametro, dentibus subulato-lanceolatis (2.6) 3-5 mm longis; petalis laete purpureis in sicco coerulescentibus; vexillo per 45° sensim recurvo late rhombico-oblanceolato 19-23 mm longo, 7.5-12 mm lato; alis 17.6-19.5 mm. longis, lamina oblongo-lanceolata subrecta 10.2-11.7 mm longa, 2.4-3.1 mm lata; carina 15.4-18.1 mm longa, laminis semi-obovatis obtusis 7.5-9 mm longis, 3.1-3.5 mm latis; legumine adscendenti-patulo saepissime humistrato sessili, maturo deciduo, late oblongo-cylindrico, oblongo-ellipsoidea vel anguste clavato-ellipsoideo, 2.5-4.5 (5) cm longo, (0.8) 1-2.1 cm lato, basi rotundato, apice abrupte cuspidato, subtereti rectoque vel leviter incurvo et tunc dorso subsulcato, valvulis primum crassissimis succulentis laevibus viridibus solem versus roseo-tinctis, demum stramineis vel brunneo-purpurascentibus subtiliter reticulatis spongiosis, endocarpio late inflexo septum completum efformanti; ovulis

(41) 45-66; seminibus ochraceis vel fuliginosis parce scrobiculatis (2.9) 3.2-3.9 mm longis.

NEW MEXICO. Gypsum flats and low gullied gypseous hills, altitude 3650 ft., 7 miles SW of White's City, Eddy Co., 17 May, 1953, *Ripley & Barneby* No. 11138. Type in Herb. Calif. Acad. Sci.; isotypes GH, NY, OKLA, POM, RM, SMU, US, WSC, WTU. 12 miles SW of White's City, *Ripley & Barneby* No. 11143 (CAS, NY). SW of Carlsbad Cavern, *Ripley & Barneby* No. 4203. TEXAS. 2 miles S of Texas-New Mexico state line, N end of Rustler Hills, Culberson Co., *H. B. Warnock* No. 5490 (SRSC). 9 miles NW of "Paso Tex," just S of New Mexico line, Culberson Co., *Ripley & Barneby* No. 11152 (CAS, NY, RM, SMU). 30 miles N of Pecos, Reeves County, *Eddie K. Norris* No. 13 (SRSC).

This striking species is found in dry flats, gullied knolls and low rolling hills, rooting in almost pure gypsum or in stiff clay soils of high gypseous content, and associated with *Anulocaulis leiosolenus* (Torr.) Standl., *Nama carnosum* (Woot.) C. L. Hitchc. and *Coldenia hispidissima* Gray. The known stations lie close together within a radius of some forty-five miles within the Pecos River valley and along creeks flowing eastward to the Pecos in southern Eddy County, New Mexico, and closely adjoining counties in Texas. It is probably a specialized derivative of *A. crassicarpus* (or of a recent common ancestor), differing from var. *crassicarpus*, of which it has the purple flower (though averaging a trifle larger), in the denser vesture of shorter strictly appressed hairs, the leaflets being often more densely pubescent above than below, in the more numerous (mostly 15-30 as opposed to 7-15) flowers to the raceme, and especially in the pod which, although somewhat variable in outline, is proportionately twice as long, fluctuating around a cylindro-oblong rather than subglobose norm.

3. A. PLATTENSIS Nutt.

Phaca plattensis (Nutt.) MacM. *Geoprumnon plattense* (Nutt.) Rydb. *A. pachycarpus* T. & G. *A. crassicarpus* var. *pachycarpus* (T. & G.) Jones. *Geoprumnon pachycarpum* (T. & G.) Rydb.

Although this well known species was first discovered on the "Plains of the Platte," probably in Nebraska, it is more abundant by far in Oklahoma and central Texas. It reaches nearly to the Gulf near Matagorda Bay in the latter state, but is apparently rare on the coastal plain. From Oklahoma it is dispersed northward in rather scattered stations to the Souris River in north-central North Dakota, westward to northeast Wyoming and eastern Colorado. I am less well informed about the eastern limit of its range. It has been collected in Iowa, and reported from Minnesota, Illinois, and Alabama, in some cases probably erroneously.

Astragalus pachycarpus was based on a plant collected on "Prairies of Arkansas" by Dr. Leavenworth, perhaps in what is now Oklahoma. The type (NY) consists of a few leafy stem-tips and a detached pod in an advanced stage of maturity, probably picked up off the ground late in the season. The leafy parts are too fragmentary for identification by themselves, but fit in well with what we know of *A. plattensis*. The pod is that of *A. plattensis* exactly, except that it is hairless. But the vesture may perhaps have been lost by weathering. Several attempts have been made to associate this old collection with a naturally occurring species, none of them successful. Gray (in Proc. Amer. Acad. 6:193) thought it might be a depauperate state of *A. caryocarpus*.

Jones (Rev. Astrag.:237) treated it as a variety of *A. crassicarpus*, but the substance of his variety is a mixture of flowering *A. crassicarpus* var. *Berlandieri* and fruiting var. *trichocalyx* in the sense of this paper. Rydberg (in Bull. Torr. Club 53:164) discussed the species at some length and, after admitting that he had seen no fruiting specimen other than Leavenworth's type, cited several collections of var. *Berlandieri*. It is reasonable to suppose that botanical exploration of Arkansas and Oklahoma has reached a point where we can discount the possibility of rediscovering a species bearing the pod of *A. plattensis*, though glabrous, in an area where *A. plattensis* itself is of common occurrence. And we can confidently lay *A. pachycarpus* to rest in the synonymy of the latter species.

ASTRAGALUS HELLERI Fenzl and A. SANGUINEUS Rydb.

These two Mexican species were referred by Rydberg to the section *Mollissimi*. It is true that *A. Helleri* (or *A. orthanthus* of most authors) resembles *A. mollissimus* Torr. and its relatives in growth and tomentose vesture, but the pod is rather that of *A. crassicarpus*. The long narrow flower with scarcely recurved scarlet petals, combined with the pod of *Geoprumnon*, entitle these species to a section of their own. It is rather likely that *A. Hartmanii* Rydb., which has similar flowers but whitish petals, belongs with them; but this is known only from the type-collection and the fruit is yet to be discovered.

KEY TO A. HELLERI AND A. SANGUINEUS

1. Herbage tomentose-silky; petals all acute, the banner entire and mucronate at apex; Puebla and Vera Cruz .... 1. *A. Helleri*
1. Herbage strigulose, the leaflets glabrous above; banner retuse at apex, the wings and keel obtuse; Coahuila and Nuevo León .... 2. *A. sanguineus*

1. A. HELLERI Fenzl in Bonplandia 6:56. 1861

A. orthanthus Gray, 1864. *A. erythrostachys* Ulbr., 1902.

I have no hesitation in adopting Fenzl's name for the species passing in our monographs as *A. orthanthus*, even though I have seen the type of the latter only. The type of *A. Helleri* was collected on the west slope of Mount Orizaba and was very fully described. Fenzl's phrases, alluding in part to plants cultivated in Vienna: "corolla fervidissime incarnata . . . vexillo acuminato redunce mucronata . . . alis acutissimis . . ." are convincing. The type of *A. orthanthus* originated near Perote, a village on the north slope of Orizaba (*Halstead* 19, NY). The type of *A. erythrostachys* was taken by Preuss in the same general district, between Perote and Tezintlán, and described as having the flowers: "magnificis maximis rubicundis fulgentibus . . . bis 3 cm. lang . . ."; and banner "plus minus acuminato." The identity of the three propositions can hardly be questioned. The species is apparently confined to the Orizaba massif in the states of Vera Cruz and Puebla, the collection from Nuevo León (*Palmer* 2137) referred here doubtfully by Rydberg (in Bull. Torr. Club 56:540) being certainly the following.

2. A. SANGUINEUS Rydb.

This species was based on a single collection, namely *Palmer* 243 (US) from "Saltillo, Nuevo León," more precisely, according to the label, from a

point "12-14 leagues south of Saltillo," hence really in southern Coahuila. In recent years the species has been traced, through ten collections, north to Sierra del Pino and Sierra de la Encantada in northwest Coahuila, and south along the Sierra Madre Oriental to Galeana district in southern Nuevo León.

Astragalus caricinus (Jones), stat. nov.

A. Lyallii var. *caricinus* Jones, Rev. Astrag. 174, Pl. 41. 1923.

This species has been repeatedly passed over as a luxuriant or large-fruiting state of *A. Lyallii* Gray, which it closely resembles in growth-habit, abundant vesture, loose racemes of tiny declined flowers, and small bilocular pod. But it differs from *A. Lyallii* in the conspicuous scarious lower stipules which are united into a contrapetiolar sheath, in the more nearly appressed pubescence of the stiffer more erect stems, while the pod is perfectly sessile, lacking the minute but evident stipe of *A. Lyallii*. The range of *A. caricinus* is apparently bicentric. The main area lies along the banks of the Snake River from central Cassia County, Idaho, downstream as far as the mouth of the Owyhee River in Malheur County, Oregon. It then reappears, mostly unexpectedly, on the lower Yakima and adjoining reaches of the Columbia River in Yakima, Benton and western Grant counties, Washington.

Astragalus scutaneus, sp. nov.

A. brazoensi Buckl. affinis, sed leguminis sessilis (nec in gynophoro elevati) valvulis tenuioribus strigulosis, racemo plurifloro, floribus paullo minoribus, ovulis magis numerosis (10-12, nec 4), aliisque notulis longe distans.

Herba caulescens validiuscula e radice verticali verosimiliter annua, pilis rectis appressis basifixis ad 0.3-0.5 mm usque longis omnibus fere partibus strigulosa, foliolis superne glabris; caulibus diffusis vel assurgentibus subsimplicibus stramineis 1.5-3.5 dm longis; stipulis submembranaceis pallidis demum scariosis triangularibus 3.5-4 mm longis semi-amplexicaulibus inter se liberis; foliis fere omnibus sessilibus foliolis 8-11-jugis oblongis oblongo-ovatis vel foliolorum superiorum lineari-oblongis truncatis retusisve 5-14 mm longis; pedunculis 3.5-6 cm longis, folio superatis; racemis dense (20) 25-40-floris, ad anthesin anguste cylindricis, floribus mox deflexis, axi fructifero paullo elongato 3-6.5 cm longo, leguminibus retrorsus imbricatis; pedicillis ad anthesin circa 0.5 mm fructiferis recurvis 0.8-1.4 mm longis; calycis 3-3.5 mm longi plerumque nigrostrigulosi tubo campanulato 1.9-2.2 mm longo, 1.7-2 mm diametro, dentibus subulatis 1.1-1.5 mm longis; petalis lilacinis vexillo saturatius purpureo-striato; vexillo obovato cuneato retuso leviter recurvo 5.2-6 mm longo, 3.7-4 mm lato; alis 5.2-5.5 mm longis, lamina oblique triangulari vel lunato-oblonga obtusa vel emarginata 4-4.2 mm longa, 1.5-2 mm lata; carina 3.9-4.4 longa, laminis semi-rotundis 2.3-2.9 mm longis, 1.6-1.8 mm latis, per 110° in apicem obtuse vel acute deltoideum abrupte incurvis; legumine deflexo sessili in receptaculo diu persistenti peltiformi, de visu dorso-ventrali late ovato vel subrotundo basi emarginato apice abrupte apiculato, fortissime obcompresso angulis lateralibus fere aliformibus, valvulis tenuiter chartaceis demum subdiaphanis stramineis vel purpureo-guttulatis lucidis transverse reticulatis parce strigulosis, endocarpio introflexo septum angustissimum sed completum 0.5-1 mm latum efformanti; ovulis 10-12; seminibus olivaceis brunneisve purpureo-guttulatis laevibus sed opacis 1.8-2.1 mm longis.

MEXICO. Sandy shore at west end of Lake Chapala, Jalisco, 14 July, 1940, *C. L. Hitchcock* & *L. R. Stanford* No. 7166. Type in Herb. Washington State College; a duplicate sheet generously donated from the same herbarium by Dr. Marion Ownbey has been divided between the writer's collection and CAS. Constancia Station, near Guadalajara, Jalisco, *Pringle* No. 11362 (US).

Pringle's collection of this strikingly peculiar *Astragalus* has been misidentified by several students of the genus as *A. diphacus* Wats., an apparently

perennial species known as yet only from the states of San Luis Potosí and Zacatecas. This differs from *A. scutaneus* in the fewer-flowered racemes of larger flowers (the keel 5-6.5 mm as opposed to 4-4.5 mm long), and in the inflated didymous pod which is emarginate at both ends and grooved along both sutures. The fruit of *A. diphacus* is also promptly deciduous when ripe and the internal cavity is divided into two plumpy turgid chambers by a septum 2.2-3 mm wide. By contrast the pod of *A. scutaneus* is long-persistent on the receptacle and so strongly compressed dorsoventrally as to become peltiform, with flattened faces and acute or acutish almost wing-like lateral angles. It is retuse at base only, and the septum, although complete, is only 0.5-1 mm wide. In its external form the pod might be likened to a dimunitive version of that of *A. pterocarpus* Wats. The relationship of *A. scutaneus* is, however, with *A. brazoensis* Buckl. of southern Texas and adjacent Tamaulipas in which the pod is almost as strongly obcompressed but obtuse on the lateral angles, of thicker texture, glabrous, and elevated from the receptacle on a stipe-like gynophore about 1.5-2.5 mm long. The ovules of *A. brazoensis* are consistently 4 as opposed to 10-12 in *A. scutaneus*.

Pugillus Astragalorum XIX: Notes on A. sericoleucus Gray and its immediate relatives

R. C. Barneby

Wappingers Falls, New York

The group of dwarf matted or pulvinate Astragali with large hyaline connate stipules, palmately trifoliolate leaves and dolabriform vesture segregated by N. L. Britton (in Britt. & Br., Ill. Fl. 2:306. 1897) as the genus *Orophaca* is readily divided into two small series. The first, consisting of *A. gilviflorus* Sheld. and *A. hyalinus* Jones, is characterized by the cylindric calyx, narrowly oblanceolate or fiddle-shaped nearly erect banner 1.5-3 cm long, and plumply ovoid, nearly beakless pod. It corresponds with *Astragalus* sect. *Triphylli* Jones, and does not directly concern us at this point. The second, with shorter campanulate calyx, recurved obovate banner mostly less than 1.5 cm long, and slenderly ovate-acuminate pod tapering into a beak about as long as the fertile body, has been treated either as a single species composed of three varieties (Jones, Rev. Astrag.:83-84. 1923) or as three species of *Orophaca* (Rydb., N. Amer. Fl. 24:310. 1929). While there is something to be said in favor of each of these arrangements neither is wholly satisfactory in the light of material at present available.

Astragalus tridactylicus, sericoleucus, aretioides and *Barrii*, to use the names which I am adopting below, are very uniform in general organization, in the form of the leaves and stipules and, so far as the incomplete evidence goes, in the pod, and the chief differential characters are to be found in the habit of growth, in size and, to some small degree, shape of the petals, and in the vesture of the stipules. These criteria are not of the first importance relative to the taxonomy of the whole genus, and it could well be argued that the taxa involved are better interpreted as of no more than infraspecific value. However, the two extreme forms, *A. sericoleucus* and *A. Barrii*, are so very different from each other, in spite of contiguous ranges at the same altitude and almost identical environment, that it seems hardly possible to unite them under one specific heading. In the whole series there appear to be (if we consider them in linear sequence) three marked discontinuities in variation of about equal width. If any one of these is considered sufficient to mark off a species from the rest, all must logically be allowed an equal measure of importance. I therefore treat the group as four species.

1. A. SERICOLEUCUS Gray, 1862

Phaca sericea Nutt. ex T. & G., 1838, not *A. sericeus* DC., 1802. *Orophaca sericea* (Nutt.) Britt., 1897.

Prostrate, the stems (eventually indurated and woody below) creeping outward from the crown of the taproot to form dense mats 1-9 dm in diameter, the leaves and short leafy spurs all disposed to one side of the distinctly caulescent stems, which are concealed by a thatch of densely pubescent stipules;

longest hairs of the herbage about 3 mm long; peduncles slender, usually developed and 5-25 mm long; racemes loosely (2) 3-5-flowered; flowers very small, the calyx 2.4-4.3 mm long, its teeth 0.6-2 mm long; banner 5.2-6.2 mm long; keel 4-4.5 mm long, the half-obovate or nearly half-circular blades 2.2-2.7 mm long, incurved through about 100° to the blunt apex; anthers 0.3-0.4 (0.45) mm long.

Exposed ridges, knolls and hilltops, on shale or limestone, about 3800-5300 ft., widespread and rather common from the head of the Republican River, Kit Carson Co., Colorado, N over the plains to the head of the White and Niobrara rivers in NW Nebraska and W, in scattered stations, up the North Platte to the Seminoe Mts. in Carbon Co., Wyoming.

2. **A. aretioides** (Jones) comb. nov.

A. tridactylicus var. *aretioides* Jones, Contrib. West. Bot. 8:13. 1898. *Orophaca aretioides* (Jones) Rydb., 1906.

Densely pulvinate, forming mounded cushions up to 1-3 dm in diameter, the stems of the year almost none or at most 1.5 cm long, commonly reduced to rosulate crowns; herbage lustrous-silky, the longest hairs about 2 mm long; stipules glabrous dorsally; leaves densely congested, the leaflets 3-6 mm long; peduncles 7-15 mm long; racemes almost consistently 2-flowered; calyx 3.3-4.2 mm, the teeth 1.2-2 mm long; banner 5.8-8 mm long; keel 4.1-4.5 mm long, the blades 2.5-2.9 mm long, incurved and obtuse as in *A. sericoleucus*.

Bare clay banks and bluffs, 4000-7000 ft., on sandstone or limestone, locally plentiful on the higher plains and foothill-canyons of the upper North Platte, Sweetwater, Wind and Big Horn rivers from near Fort Steele, Carbon Co., Wyoming to S Big Horn Co., Montana.

Apparently most nearly related to *A. sericoleucus*, the present species differs in growth-form, dorsally glabrous stipules and fewer slightly larger flowers. Its range of dispersal lies further to the west at greater altitudes. The type was collected by Henry Engelmann on Simpson's Expedition, August 19, 1858, on "mountains near the Sweetwater River." The name was subsequently transferred by Jones to the better known mat-forming phase of *A. tridactylicus* common on the Laramie Plains, which differs in growth-form, densely pubescent stipules and considerably larger and more numerous flowers.

3. A. TRIDACTYLICUS Gray, 1865

A. sericoleucus var. *tridactylicus* (Gray) Jones, 1902; *Orophaca tridactylica* (Gray) Rydb., 1906. *A. tridactylicus* fma. *coloradoensis* and fma. *pallidiflora* Gand., 1902.

Typically acaulescent and tufted, becoming somewhat matted at high altitudes, but the growth of the year commonly reduced to rosulate crowns; longest hairs about 2 mm; stipules all, or at least the early ones (subtending the shorter leaves) pubescent dorsally; leaves often dimorphic, the early ones (sometimes all) quite short and with obovate or broadly cuneate-oblanceolate leaflets up to 1.3 cm long, the later ones developing with or after the flowers longer, with slender petioles and longer narrowly oblanceolate leaflets up to 2 cm long; peduncles all much shorter than the leaves, sometimes included in the sheathing stipules; racemes (2) 3-6 (10)-flowered; calyx 4.5-6.9 mm long, the teeth 1.8-3.5 mm long; banner 8.3-11.6 mm long; keel 5.3-7.2 mm long, the

blades 2.8-3.6 mm long, incurved through at least 90° and usually more to the rounded or bluntly deltoid apex; anthers 0.35-0.55 mm long.

Plains, bluffs and knolls, in gravel, sand or clay derived from shale, sandstone or limestone, sometimes abundant on red beds (Chugwater formation), 4800-7300 ft., common and locally abundant along the Rocky Mountain piedmont from near Denver, Colorado N to the Platte River valley near Casper, Wyoming.

Astragalus tridactylicus differs consistently from the two preceding in its larger flowers. The strictly typical form, known only from the foothills of the Colorado Rocky Mts., from Denver N to Larimer County (perhaps immediately adjacent Wyoming), is acaulescent and tufted, with strongly dimorphic leaves, and the inner stipules subtending the longer leaves tend to be glabrescent dorsally. On the Laramie Plains and on bluffs and knolls along the North Platte from Platte to Natrona County, Wyoming, the plants are more matted, all the stipules are densely pilose dorsally, and the leaves differ little according to sequence in the cycle of growth. It is to this latter form that the name *A. tridactylicus* var. *aretioides* is commonly although (as shown above) erroneously applied. It may perhaps deserve varietal status.

4. **Astragalus Barrii**, sp. nov.

A. tridactylico Gray floribus majusculis habituque caespitoso proxime affinis, sed floribus et majoribus (calycis tubo 3.6-5 mm, nec 2.7-3.5 mm longo; vexillo saepissime 10.5-16.7 mm nec 8.3-11.5 mm longo; carina 7.5-10.5 mm nec 5.3-7.2 mm longa), stipulis omnibus dorso glabris, necnon carinae laminis per 60-85° tantum in apicem triangularem acutum sensim incurvis absimilis.

Densely tufted or mounded, the stems of the year reduced to leafy crowns elevated year by year on the divisions of a closely forking suffruticulose caudex, forming low cushions up to 1.5 or exceptionally 4.5 dm in diameter; herbage silvery-strigose with dolabriform hairs up to 1-1.4 mm long; stipules 4-8 mm long, glabrous dorsally; leaves 1-4 cm long, the 3 leaflets linear-oblanceolate, oblanceolate or elliptic-obovate acute or acutish, 3-12 mm long; peduncles slender 7-16 mm long, shorter than the leaves; racemes loosely (1) 2-4-flowered, the fruiting axis up to 5-15 mm long; calyx (4.8) 5.5-7.1 mm long, the deeply campanulate or subcylindric tube 3.6-5.1 mm long, the teeth (1.2) 1.5-2.4 mm long; petals pink-purple, the obovate-cuneate or broadly oblanceolate banner (9.6) 10.5-16.7 mm long; wings 9.1-13.5 mm long, the claws 4.1-5.5 mm, the linear-oblong or obliquely obovate blades (4.6) 5.3-8.5 mm long; keel 7.5-10.5 mm long, the claws 4.3-6 mm, the lunately half-elliptic blades 3.5-4.8 mm long, 1.6-2.5 mm wide, gently incurved through 60-85° to the triangular acute apex; anthers (0.45) 0.5-0.7 mm long; pod narrowly lance-ellipsoid, 4.5-6.5 mm long, 1.2-1.8 mm in diameter just above the rounded base and thence tapering into a slightly incurved lance-subulate beak about as long as the fertile portion, obscurely triquetrous in the lower half, somewhat flattened dorsally, the valves papery, silvery-strigulose; ovules (7) 9-11; seeds (often only one maturing) oblong, scarcely compressed, dull purplish-green, smooth but not lustrous, about 2 mm long.

Gullied knolls, buttes and hilltops, in calcareous gravelly clay soils, below 5000 ft., apparently rare and scattered, on and near the White-Cheyenne River divide in SW South Dakota, and about the headwaters of the Powder River in NE Wyoming and adjacent Montana.

Specimens examined.—SOUTH DAKOTA. Limestone Butte (SE of Oelrichs), Fall River Co., May 4, 1952, *Claude A. Barr.* Type in herb. Calif. Acad. Sci. Kennedy's Butte, Fall River Co. (T9, R9), 2 mi. SE of Prairie Gem Ranch, May 6, 1952, *Claude A. Barr.* Cedar Butte, Shannon Co., April 29, 1952, *Claude A. Barr.* WYOMING. Buffalo, Johnson Co., *Tweedy* 3256 (N. Y. Bot. Gard.). MONTANA. Butte Creek, Powder River Co., *Mrs. Considine* (herb. Barr.).

It is a pleasure to associate this delightful little *Astragalus* with the name of Claude A. Barr, keen observer and successful cultivator of the prairie and badlands floras, who through the medium of his nursery at Prairie Gem Ranch near Smithwick has done much to introduce to gardeners here and abroad the beauties of the native vegetation. *Astragalus Barrii* first came to my attention in the form of living plants received from Prairie Gem under the name *A. tridactylicus.* Being already familiar with the latter, I was much puzzled by their identity. Later, at my request, Mr. Barr kindly supplied excellent herbarium specimens, both wild and cultivated, together with a large old plant showing the nature of the root and caudex. Mr. Barr has himself written engagingly and informatively of the cushion Astragali of the Plains (Bull. Amer. Rock Garden Soc. 9:2-4. 1951). This article is illustrated with two clear photographs of *A. Barrii* (under the name *tridactylicus*) in its native haunts.

Astragalus Barrii is evidently closely related to *A. tridactylicus,* differing principally in the glabrous stipules and large flowers. The calyx-tube is also longer, sometimes subcylindric or at least quite deeply campanulate, and the keel-petals are much less strongly incurved and sharply triangular at apex. Like typical *A. tridactylicus* it forms low cushions or mounds, but the leaves are not strongly dimorphic. Although we know of it at present in only two restricted areas to the southeast and northwest of the Black Hills, it is to be expected in intermediate stations, wherever the required habitat of bare limestone hilltops is available. Its area of dispersal lies to the north and northeast of that of *A. tridactylicus,* at slightly lower elevations. It should be added that *A. tridactylicus* toward its northern limit (nearest to *A. Barrii*) is represented by populations of the mat-forming type, very small-flowered and with densely pilose stipules. The gap between the two is sharply marked geographically and morphologically.

Book Reviews

Vascular Plants of Illinois. By George Neville Jones and George Damon Fuller, prepared with the collaboration of Glen S. Winterringer, Harry E. Ahles, and Alice A. Flynn. The University of Illinois Press, Urbana, Illinois. 593 pp., 1375 maps. 1955. $10.00.

This noteworthy contribution to the flora of one of the midwestern states has been eagerly awaited. It represents the effort of many years of preparation, originally undertaken at the University of Illinois in 1939 by Dr. Jones, who is mainly responsible for the text. Later, Dr. George D. Fuller, who had retired from active teaching in Ecology at the University of Chicago, initiated an herbarium at the Illinois State Museum at Springfield, and joined Dr. Jones in the project. Dr. Fuller was assisted later, both in the field and herbarium, by Dr. Winterringer, while Dr. Jones from the beginning has been tremendously aided by Dr. Ahles and Mrs. Flynn, so that the total production is the result of the continuous labor and capabilities of all these botanists.

The purpose of the work "has been to present a systematic, phytogeographical, and bibliographical enumeration of the native and adventive vascular plants known to grow spontaneously in Illinois, and to show graphically their geographical distribution within the state by means of outline-maps, or by cited specimens available for reference in public institutional herbaria." In these particulars the book has certainly accomplished its aim. About 2450 species are treated as valid in the book. The sequence of families and orders followed is essentially that of Engler & Prantl. For the greatest facility of reference the genera within the family and the species within the genus are treated alphabetically.

To this reviewer the chief weakness of the book is the attitude taken by the authors with respect to varieties and forms. All subdivisions of the species are automatically relegated to synonymy, based on the authors' contention that "many of these have in all probability little or no permanent value," and that since "species are composed of several or many races or 'varieties'," the "species includes all its varieties, whether or not these have been named." While most taxonomists would agree to the general principle here expounded that the whole [species] is made up of the sum of its parts [varieties and forms], the attitude taken by the authors of treating all varieties and forms as synonyms will be upheld or followed by few taxonomists. Even though critical and carefully executed monographic work has resulted in the separation of varietal and formal taxa, the authors of the Vascular Plants of Illinois do not feel justified in recognizing such segregates except insofar as these segregates are relegated to synonymy. The result is that varieties and forms are equally assigned to synonymy and the reader has no choice to judge whether the authors of this work would view any particular subdivision of a species as "good" or "bad." Nevertheless, in 1943 Dr. Jones deemed a pubescent-leaved variation of *Prunus virginiana* important enough to describe and publish it as forma *Deamii* (Rhodora 45:355), but in the present work this is thrown into synonymy. Automatically, the large and small-flowered Yellow Lady's Slipper are cast into *Cypripedium parviflorum*, yet in order to have been consistent with their attitude that a species consists of its varieties, the authors should have used the earlier and more inclusive name, *Cypripedium Calceolus* L. of Europe, under which *C. parviflorum* is now treated as a variety by orchid specialists and by the standard floras published by Fernald and by Gleason. Moreover, there are many examples of other varieties which have been recognized as sufficiently distinct to be followed by most botanists. Yet, these are all placed in synonymy indiscriminately, the "good" listed along with the "bad." Conversely, some taxa, such as *Boehmeria cylindrica* var. *Drummondiana* and *Asarum canadense* var. *acuminatum*, which are treated in most modern floristic works as varieties, in the present work are maintained as valid species, a position with which most botanists will not be in agreement. Furthermore, some of the generic names used in the present work, such as *Oxycoccus* rather than *Vaccinium*, and *Chamaesyce* as distinct from *Euphorbia*, will not be accepted by most botanists.

Due to the limitations of space, keys are not provided in the present work. Instead, for the identification of his plants, the reader is referred to Jones's Flora of Illinois (second edition, 1950), in which simple keys are provided. The maps are well reproduced. In order to conserve space, two species are sometimes indicated on the same map. The type

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